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Studies on a Kentucky Knobs Lake. IV

Some Limnological Conditions during an Unusually Cold Winter[1]

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ABSTRACT

Physical and chemical conditions in Tom Wallace Lake, Kentucky, were studied through three intermittent ice covers for a period of 49 days during January and February 1958.

A Birgean heat budget, based on temperatures observed from a station over the deepest part of the basin, involved a loss of 80 g-cal/cm^2 for the entire period. However, temperature profiles made from several stations revealed that there was considerable vertical and horizontal turbulence within the water mass beneath the ice, and that isotherms were not horizontal.

Although temperatures of the sediment and deep waters fluctuated, the direction of heat flow from the thin layer of profundal sediment was always upward into the overlying one or two meters of water. Most temperature changes at mid depths, especially at 5 m, were probably caused by lateral transport of heat, since vertical thermal gradients were nonexistent or very slight at those levels. The direction of thermal gradients in the uppermost one or two meters beneath the ice was more varied. At times heat seemed to be moving downward from the ice; at other times an inverse gradient was observed even though the upper water was gaining heat.

On several days the vertical temperature profile could not be reconciled with the density of water as a function of the prevailing temperatures, and in a few instances these anomalous stratifications could not be correlated with available chemical data. Some relative-density determinations of water from different depths showed on one occasion that there was no instability in spite of an anomalous temperature profile.

Freezing-out effects during times of ice formation, and diluting caused by rain and melting were reflected beneath the ice in changing values of total alkalinity, total iron, and total solids.

Stratification and variation in values of dissolved oxygen, total alkalinity, iron, and total solids are discussed.

INTRODUCTION

Unusual limnological conditions were observed in Tom Wallace Lake, Jefferson County, Kentucky, between January 5 and February 23, 1958. The borderline climatic region in which Tom Wallace Lake lies is such that the lake is monomictic during years with mild winters, and dimictic when winter conditions permit brief ice covers. However, there were four periods of circulation interrupted by three separate, complete ice covers during January and February 1958.

Although such multiple mixing does not conform with the definition for *polymictic* lakes suggested by Hutchinson and Löffler (1956), we believe that polymictic is the best descriptive term for Tom Wallace Lake between the summer stagnation periods of 1957 and 1958. The logical sequence for descriptive prefixes for mixing of waters in

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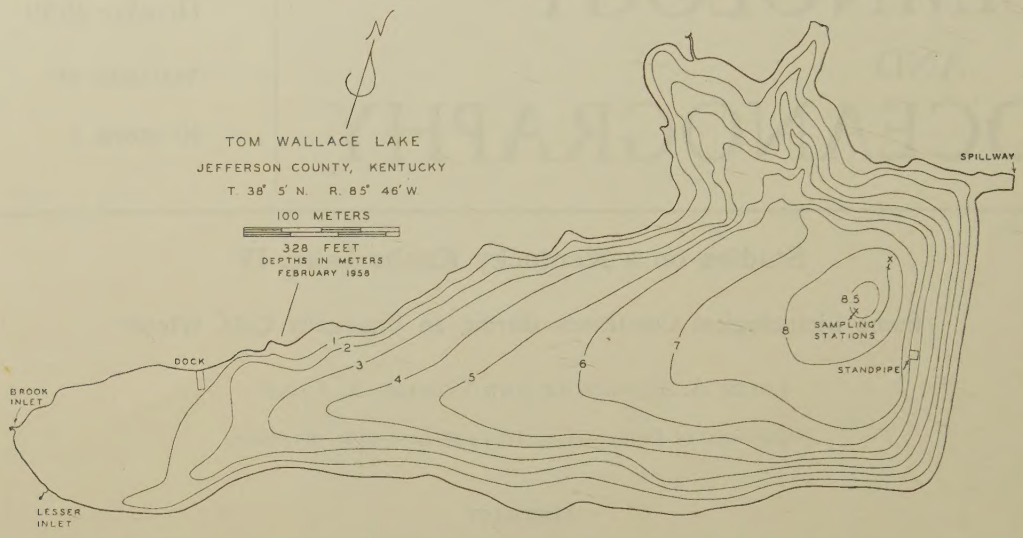

FIG. 1. Bathymetric map of Tom Wallace Lake.

TABLE 1. *Morphometric data from Tom Wallace Lake, Jefferson County, Kentucky*

Area	2.34 ha
Volume	90,647 m³
Shoreline	880 m
Maximum depth	8.75 m
Mean depth	3.9 m
Volume development	1.33
Shoreline development	1.62

Depth m	Area ha	Volume	
		Stratum	m³
0	2.34	0–1	21,460
1	1.96	1–2	17,990
2	1.64	2–3	14,980
3	1.36	3–4	12,280
4	1.11	4–5	9,775
5	0.85	5–6	7,195
6	0.60	6–7	4,645
7	0.34	7–8	2,090
8	0.10	8–8.5	225
8.5	0.01	8.5–8.75	7
8.75	—		

lakes is *mono*mictic for circulation only once a year, *di*mictic for circulation twice a year, and *poly*mictic for circulation more than twice a year. The first two terms are well established in the literature. It would be unfortunate if the useful adjective polymictic were limited to description of specific situations where daytime stratification is destroyed each night, as implied by Hutchinson and Löffler.

Some environmental and biotic factors of Tom Wallace Lake have been discussed in four earlier papers (Distler 1952; Cole 1954, 1957; and Neff 1955). The lake is an artificial impoundment in a wooded ravine among the typical conical hills of the Kentucky physiographic province called the Knobs. It is located at 38° 05′ N and 85° 40′ W at about 600 feet above mean sea level.

In 1954 Cole presented a bathymetric map and some morphometric data from Tom Wallace Lake. During the ice cover of 1958, a series of 320 soundings was made through the ice at carefully measured intervals. From those soundings a new map was prepared (Fig. 1), and it supersedes the earlier one based on soundings made from a boat. Morphometric details derived from the new map (Table 1) were used in calculating heat budgets.

Hayes (1957), in presenting some data concerning the morphometry of 500 lakes, stated that the average ratio of maximum depth to mean depth was 2.35 for those lakes for which data are available. In Tom Wallace Lake that ratio is 2.24. One may infer from Hayes' data that the average lake considered in his paper has a volume development of 1.27, very close to the 1.33

of Tom Wallace Lake. Moreover, Hayes showed a curve in which mean depths of many lakes were plotted against their areas on log-log paper. He presented a formula for the slope of the central part of the curve, and suggested that an extrapolation of the relationship into shallow ponds might be justified, although the lakes with areas less than 0.3 km^2 plotted on his graph did not show this. Tom Wallace Lake is similar to Hayes' small, shallow lakes; it cannot be fitted to the curve with his formula, and would lie on the lower left-hand part of the graph along with Hayes' shallow lakes, which average 3.6 m in depth and which show no obvious increase of depth with area. From these observations we are led to conclude that the man-made Tom Wallace Lake shows no unusual morphometric features.

During January and February there were two major inlets at the upper (west) end of the lake. One of these was an intermittent brook that flows from a wooded ravine almost every winter. From a smaller wooded ravine at the southwest corner of the lake, a second stream entered the lake about 75 feet from the mouth of the brook inlet. The second stream, termed the lesser inlet, had not been observed by us before, and must be dry during most years. Calculations were made of the rate of flow of both inlets; the brook inlet poured water into the lake at the approximate rate of 430 m^3/day, and the lesser inlet at a rate of about 195 m^3/day. For about seven days, when it was frozen solid, the lesser inlet contributed nothing to the lake. Although those two inlets and precipitation seemed to be the main sources of lake water, seepage of ground water probably played an important role. In some places at the shallow margins of the lake, gelatinous, rusty masses could be seen lying on the bottom. Those rusty areas disappeared whenever the ice melted and turbulence due to wind occurred. Probably those masses were composed largely of precipitated ferric hydroxide which had entered the lake by seepage. There is little reason to doubt that seepage occurred at lower levels down the basin slope, and, in fact, many of the phenomena observed under the ice during the period of investigation can be explained best by assuming the entrance of subsurface ground water.

A concrete spillway at the northeast corner of the lake is the only outlet. During the study period some water flowed over the spillway at all times, although the flow was scanty on the coldest days.

Some climatological conditions prevailing during this study are shown in Figure 2. The data were taken from U. S. Weather Bureau reports from the station at Standiford Field, Louisville. The station is located approximately seven miles north of Tom Wallace Lake at an elevation of 474 feet. The temperature and precipitation during January and February were well below normal; it was the coldest February in Louisville since 1905, and the coldest of any month since January 1948. There were only nine days during January and February when air temperatures at Standiford Field did not fall to 0°C. The conditions at the lake were probably more severe. On several occasions when air temperatures at Standiford Field were above freezing, those at Tom Wallace Lake were below freezing. Such differences were especially obvious toward dusk when temperatures at the lake fell rapidly.

We are grateful to several persons for assistance during the study. Professor P. J. Christian and Messrs. Harold S. Cavanah, Dewey L. Bunting II, Gene C. Blankenbaker, and Earl C. Woodside helped in the collection of data and in mapping the lake. Paul X. Callahan was most generous with his time and suggestions in measuring water densities. Professor W. H. Spragens gave valuable counsel regarding the mathematical treatment of some of the data.

HISTORY OF ICE COVER

On the night of January 2–3 or 3–4, the lake froze over completely, and the ice cover persisted until January 19 when part of the lake became open. Estimates of the percentage of ice cover (Fig. 2) were made from rough sketches prepared in the field. There was a steady decline in the percentage of ice cover from January 19 until February 1 when the ice was all gone. However, on the night of February 3–4 the lake froze over

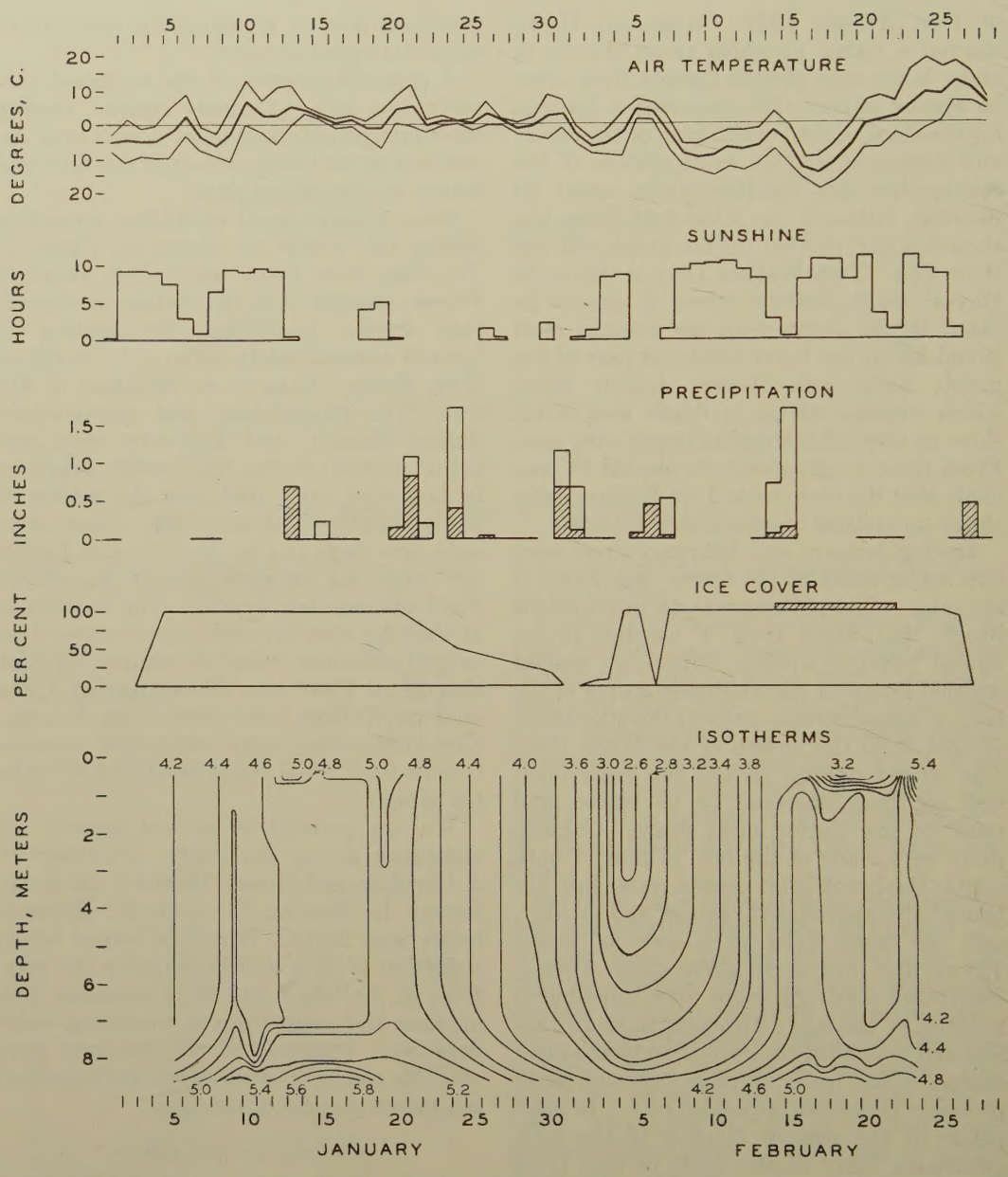

FIG. 2. Maximal, average, and minimal air temperatures; hours of sunshine; and inches of precipitation (clear areas, snow; cross-hatched, rain) at Standiford Field Weather Station, and percentage of total ice cover (snow cover shown cross-hatched); and isotherms at main sampling station, at Tom Wallace Lake, January and February 1958.

again, and by morning it was completely covered with ice about one-half inch thick. It rained heavily on February 6 and we believe that the ice melted completely. On February 8, there was a new but incomplete ice cover. By February 11, the ice cover was complete and was 4½ inches thick. That cover persisted until late February and increased in thickness to at least 6½ inches. On February 26, the ice was extremely soft and weak and disappeared rapidly during the next day.

METHODS

Water temperatures (Fig. 2) were taken with a Whitney electrical-resistance underwater thermometer calibrated to the nearest 0.2°C, and standardized against a mercury thermometer calibrated to 0.1°C. The Whitney thermometer was found to be accurate, and readings of about 0.05°C could be made by interpolation. The temperatures of the sediments were determined by allowing the thermal element to sink vertically into the mud, although it is not known how far it sank into the sediments nor how that depth varied with different bottom types.

Dissolved oxygen (Fig. 3) was determined by the Alsterberg modification of the Winkler Method. Titrations were delayed for

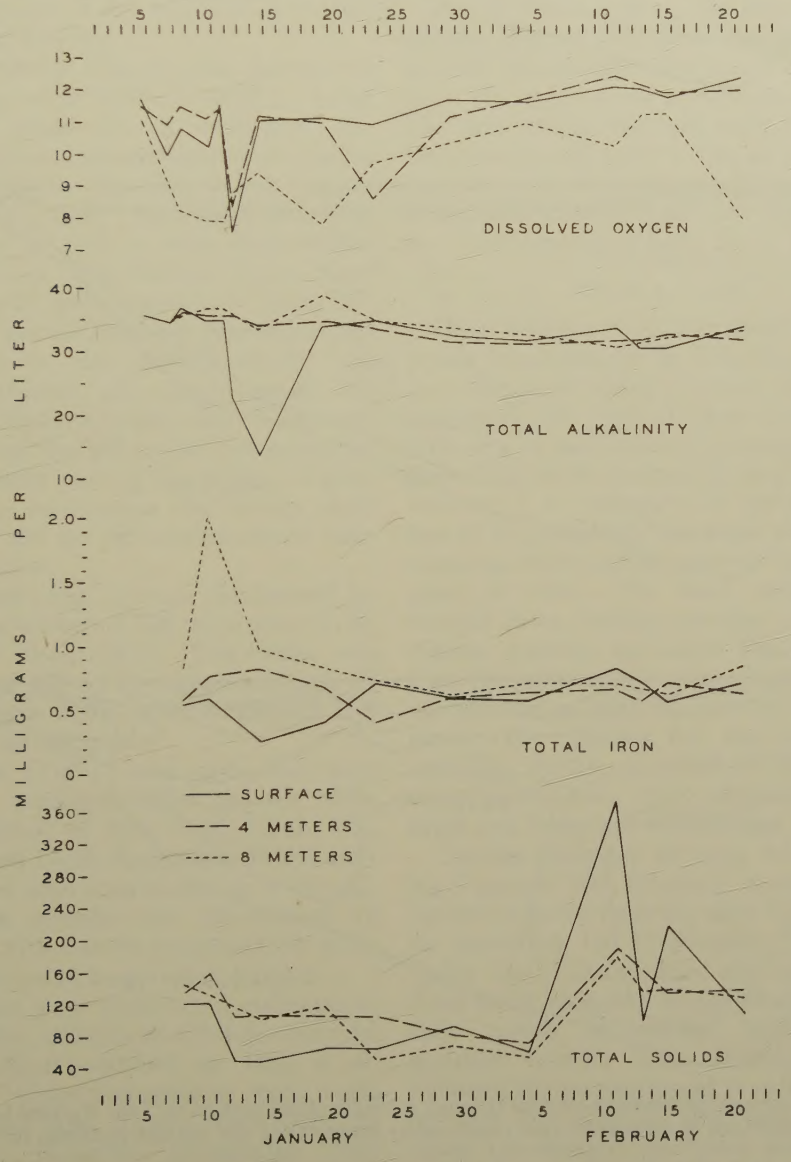

FIG. 3. Values for dissolved oxygen, total alkalinity, total iron, and total solids at depths of 0, 4, and 8 meters, Tom Wallace Lake, January and February 1958.

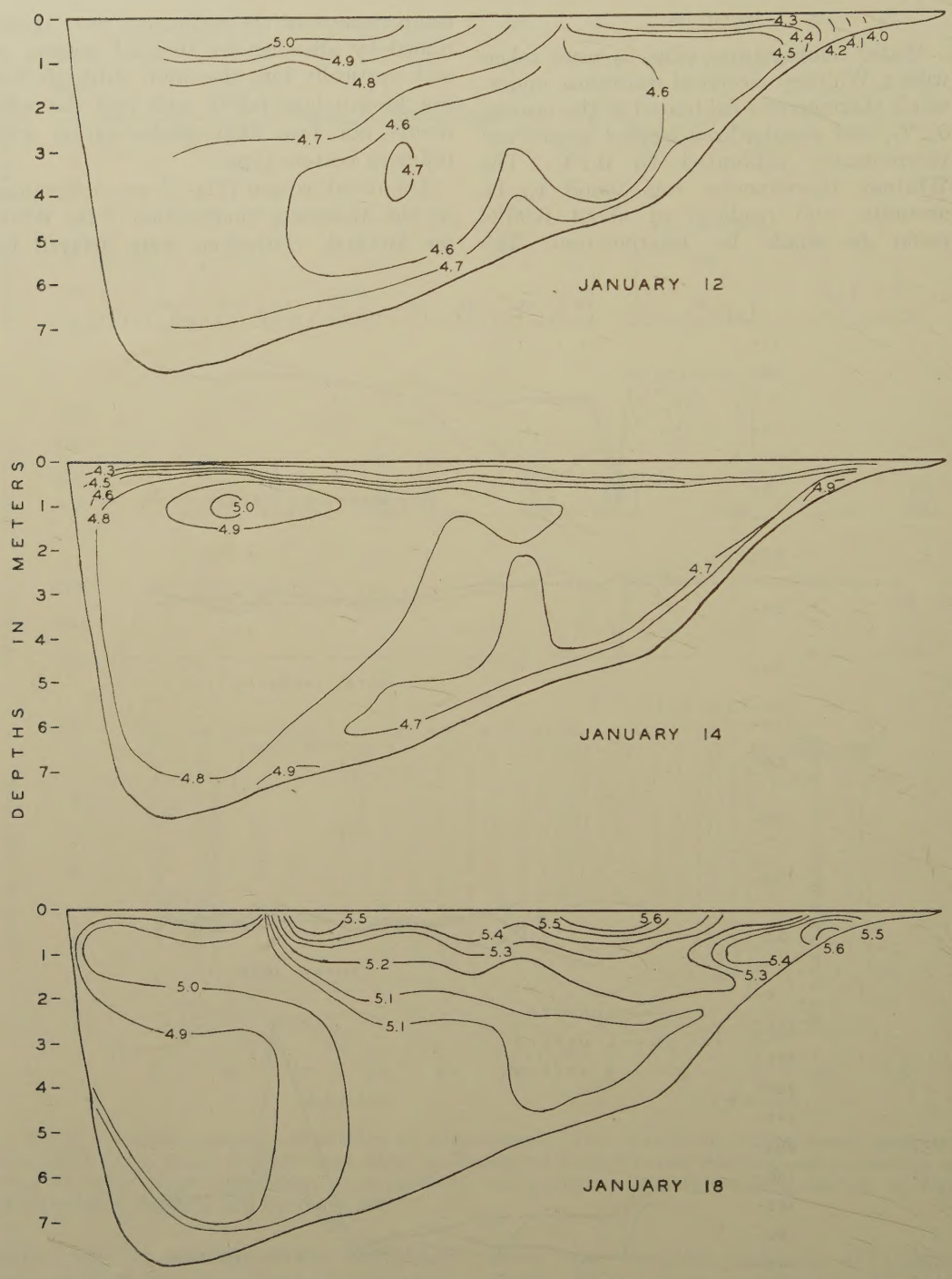

FIG. 4. Vertical temperature profiles through a longitudinal section of Tom Wallace Lake, January 1958. Temperatures of sediments were consistently higher than the nearest isotherm in the overlying water.

several hours in some instances, but the fixed samples were usually kept at least as cool as the lake water while in the field, and were stored in a refrigerator on being returned to the laboratory. A check on duplicate oxygen samples from the lake, titrated at different time intervals up to 45 hours, revealed no appreciable error introduced by this delay. One acidified sample stored in a refrigerator and titrated 45 hours later than a duplicate showed a gain in dissolved oxygen of 0.3 mg/liter, a change of 0.0067 mg/liter/hr.

Total alkalinity (Fig. 3) was determined by titrating with 0.02 N H_2SO_4, using brom-cresol green as an indicator. Alkalinity, expressed as milligrams of $CaCO_3$ per liter, probably was due to bicarbonate alone. Cole (1954) reported carbonate alkalinity to be only a rare, summertime phenomenon in Tom Wallace Lake. Further evidence that carbonates were not present was gained from pH determinations made early in the present study. An analytical pocket pH meter, made by Analytical Measurements, Inc., Chatham, N. J., showed the pH to be circumneutral during the early part of the study. Unfortunately, the instrument was broken early in January, and no pH measurements were made thereafter.

Total solids (Fig. 3) were determined by the slow evaporation of 100 ml of water in an oven set at about 96°C. The water was evaporated in 100-ml Pyrex beakers, and all weighings were made with a Mettler H-5 Multi-Purpose Balance.

Total iron (Fig. 3) and ferric iron were determined colorimetrically by the thiocyanate method of Ellis *et al.* (1948: 72). A Bausch and Lomb Spectronic 20 Colorimeter was used with a wave setting of 480 mμ. The iron in samples was determined by comparison with a curve prepared from readings of solutions of known iron content.

Phosphates were determined colorimetrically by the phosphomolybdate-stannous chloride method outlined by Ellis *et al.* (1948: 79). Color comparisons were made on a Bausch and Lomb Spectronic 20 Colorimeter. However, phosphates were determined on samples from one day only.

Data were collected at various times to determine to what extent changes occurred between day and night. On some days, data were gathered in the afternoon, at midnight, and before dawn. The variation was so slight within a 24-hour period that the time of day seemed to be of little significance. However, the exact number of hours between collections was used in calculating rates of change of various chemical and physical factors.

Except for collecting the data for longitudinal (Fig. 4) and transverse temperature profiles, all samples were taken at two stations above the deepest depression (Fig. 1). The first station was used until January 19, and was located over 8.3 m of water; subsequent data were assembled from a station a few meters south of the first station where the water was 8.6 m deep.

HEAT BUDGET

Heat budgets were calculated by multiplying temperatures at different depths by the volume of water at those depths, and expressing the sum of those products per unit area of lake surface (Birgean heat budget). The heat budget of the lake from January 5 to February 23 involved a net loss of 80 g-cal/cm^2, but there were definite warming and cooling periods during that span of time. The heat budgets were derived from vertical profiles at the two regular stations, but since Figure 4 shows that the isotherms were not horizontal, the calculations of heat budgets are subject to error. The profiles for the longitudinal axis (Fig. 4) did not intercept either of our sampling stations. Our calculations of heat gains and losses are summarized in Table 2.

Calories delivered by solar radiation during January and February were estimated by interpolation from the data of Perl (1935) as presented by Hutchinson (1957: 371, Table 36). Those data are estimates of total direct radiation on the fifteenth day of each month at various latitudes. The weather records from Standiford Field included the percentage of possible sunshine for each day (Fig. 2), and, with that additional information, estimates were made of total energy delivered via solar radiation at

FIG. 5. Aerial photograph of Tom Wallace Lake, 1:45 PM, January 8, 1958, showing ice cover and shadows cast by trees on adjacent knobs.

Tom Wallace Lake. During January it amounted to about 1,598 g-cal/cm^2. This is actually too high, because during that month the south margin of the lake was in continuous shade (Fig. 5). During February, the shaded area was of much smaller extent. Solar radiation from February 1 to February 23 contributed about 3,442 g-cal/cm^2. These figures are not particularly significant when it is remembered that reflection from the snow cover and absorption by the upper layer of ice, as well as reflection from the ice and water surface, were occurring continually.

The mean temperature of the brook inlet for the entire study period was 4.3°C. Thus, based on the calculated rate of flow, the mean internal energy content of the brook inlet was about 1,849 $\times$ 10^6 g-cal/day, or 90,601 $\times$ 10^6 g-cal during the entire period. The lesser inlet had a mean temperature of 3.6°C, but there was a period of seven days when it was frozen solid. Assuming it flowed 42 days at the calculated rate, it carried 29,484 $\times$ 10^6 g-cal. We do not know the route taken by the inlet waters upon entering the lake, nor can we theorize much concerning its role in heat transfer. Assuming density relations as a function of temperature alone, inlet waters were lighter than the water at a depth of 0.5 m in the lake except on three occasions. In those instances inlet water might have been able to move into the deeper parts of the basin with warming or cooling effects. On January 15, when the lake was ice-covered, the temperature of the dense inlet water would have had a cooling effect. The same can be said for January 22 when the sampling station was free from ice, although

TABLE 2. *Heat budget, Tom Wallace Lake, Jefferson County, Kentucky, January–February 1958*

Internal energy of inlets Referred to 0°C and to unit area of lake surface	
Brook inlet	387 g-cal/cm²
Lesser inlet	126 g-cal/cm²
Total	513 g-cal/cm²
Internal energy of outlet Referred to 0°C and to unit area of lake surface	
Spillway	475 g-cal/cm²

	g-cal/cm² involved in freezing and melting		
Date	Thickness in.	Freezing	Melting
Jan. 5	2	406	
Jan. 9	4	406	
Feb. 1	0		812
Feb. 4	0.5	101	
Feb. 6	0		101
Feb. 11	4.5	914	
Feb. 16	6	305	
Feb. 22	6.5	101	
Feb. 27	0		1,320
Total		2,233	2,233

Date	Sunshine hours	Solar radiation g-cal/cm²	Average daily mean air temperature °C	Birgean heat budget of lake water g-cal/cm²		
				Gain	Loss	Mean rate per day
Jan. 5–19	66.6	1,498	0.8	263	—	18.5
Jan. 19–Feb. 4	24.2	568	0.01	—	1,016	64
Feb. 4–16	71.8	1,680	−5.6	618	—	51
Feb. 16–21	44.3	1,012	−6.7	—	161	33
Feb. 21–23	12.5	282	3.6	216	—	98
Total	219.4	5,040		1,097	1,177	

others areas of the lake were covered. However, under the new ice cover of February 4 the brook inlet was 3.9°C and the lesser inlet was 4.3°C. The mean temperature of the lake was only 2.8°C at that time. Therefore, dense inlet water could have had a warming effect, and this may explain, in part, the rapid warming of the entire water mass under the ice in ensuing days.

On days when inlet waters were of a lesser density than the lake water at 0.5 m, they were warmer than the lake about half the time and colder the other half. In most cases the relative temperatures of inlet waters were not correlated with cooling and warming periods of the lake.

The average temperature of the spillway water was 3.8°C. If one assumes the same volume of water left the lake as entered it, the internal energy content of spillway waters was $111{,}188 \times 10^6$ g-cal during the entire period. In Table 2, the internal energy contents of the inlets and the outlet are referred to unit area of lake surface.

Calories involved in the freezing of water and the melting of ice can be calculated from estimates of ice thickness at various times. When the study started, there was an ice cover about two inches thick. By January 9 it had doubled in thickness involving about 406 g-cal/cm². That ice was all gone by February 1, the melting having required 812 g-cal/cm². The freeze of February 3–4 resulted in a cover about one-half inch thick, involving 101 g-cal/cm². That ice probably disappeared on February 6. The last freeze resulted in the gain of 4½ inches of ice by February 11, involving 914 g-cal/cm². By February 22, the ice cover was about 6½ inches thick, the increase since February 11 involving 406 g-cal/cm². That ice was gone completely by February 27. It required 1,320 g-cal/cm² to melt that amount of ice.

The first warming period under the ice was sampled from January 5 to January 19, a period of 14.25 days. The average of the daily mean air temperatures was about

0.8°C. There were 66.6 hours of sunshine, about 45.5 per cent of the possible solar radiation. The gain in the heat of lake water was 263 g-cal/cm², and the average rate of warming was, therefore, 18.5 g-cal/cm²/day. The temperature gradient beneath the ice at the sampling stations indicated that heat was moving downward from the ice to a depth of 3 m during the first half of this period. The temperature gradient was reversed on January 14 following a day of rain and melting, and heat was lost from the upper meter of water beneath the ice, but our data from January 19 again suggest a downward transfer of heat from 0.5 m to 4 m. There was a net gain at all levels during the two-week period.

From January 19 to February 4 there was a loss of 1,016 g-cal/cm². During those days, the ice cover melted completely and a new one was formed at the end of the period. This heat budget was based on temperatures recorded at the station above the deepest depression, but, because there was a partial ice cover during much of that time, and water beneath the ice was somewhat warmer at the open station, the calculations are subject to that error. However, based on our data at the open station, the average loss was 64 g-cal/cm²/day. The average of the daily mean air temperatures throughout those days was 0.01°C at Standiford Field. There were 24.2 hours of sunshine, about 14.5 per cent of the possible solar radiation. During that period, the ice melt required 812 g-cal/cm² and heat was lost at all levels of the lake and the underlying mud.

From February 4 to February 16 the water warmed beneath the ice in the amount of 618 g-cal/cm², a rate of gain that amounted to 51 g-cal/cm²/day. The average of the daily mean air temperatures at Standiford Field during that period was −5.6°C. We believe that the ice of February 4 melted on February 6 and reappeared as a complete ice cover within, at most, five days. If so, there was probably a short cooling period which our data do not show. However, there were 71.8 hours of sunshine, about 56 per cent of the possible maximum, and there was no snow cover. It would appear that the gain in heat within the lake could be attributed to solar radiation through the ice, and possibly to calories brought in with inlet waters, but the thermal gradient at the times we made our temperature determinations suggested that heat was leaving the lake through the upper layers of water and the ice. Yet, during those 12 days there was a net gain in heat in water at all levels, and the rate of heating was greater in the upper meter of water than during the January heating period when thermal gradients suggested heat moving downward from water just below the ice. By February 16, the ice cover had increased in thickness to six inches. Perhaps some of the heat (about 1,200 g-cal/cm²) released in the formation of that ice was gained by the underlying water.

Between the sampling times on February 16 and 21 there was a loss of heat. The lake lost 161 g-cal/cm² in that 4.75-day period at the approximate rate of 33 g-cal/cm²/day. Air temperatures were extremely low during that time (Fig. 2), the average of the daily mean air temperatures being −6.7°C, and the ice thickness increased one-half inch. Although solar radiation was greatest during those days with 44.3 hours of sunshine which was 81 per cent of the total possible, a thick snow cover was present (Fig. 2). Also, it was during that time that the lesser inlet was frozen, and there were no caloric gains possible from that source.

The last warming period occurred from February 21 to 23. The average of the daily mean air temperatures was about 3.6°C, and the mean daily solar radiation was 6.3 hours, 56.5 per cent of the maximum. Snow cover was absent, and both inlets were flowing. The heat gain amounted to 216 g-cal/cm², at the mean rate of 98 g-cal/cm²/day. On February 23 the water at 0.25 m below the surface was 5.45°C, and, based on thermal gradients, heat seemed to be moving downward to the 2-m level. This was believed to show the effects of solar heating through the ice. On February 26, the water flowing over the spillway had the highest temperature recorded there, 5.5°C. After February 23, the ice was not strong enough to support the

investigators. It had melted completely by February 27.

WATER MOVEMENTS AND MECHANISMS OF HEATING

Apparently the waters of the lake were constantly moving throughout January and February 1958. The movement was considerably greater when there was open water subject to agitation by the wind than when there was a complete ice cover. However, turbulence beneath the ice was very evident (Fig. 4). Although much of this turbulence could have been caused by the flow of water from the inlets, the fact that we were dealing with temperatures very near that of the maximum density of water must not be overlooked. Perhaps at such temperatures relatively small changes in the amounts of dissolved gases or solids cause more marked movements of density currents within the water mass than those caused by slight changes in temperature. It seems reasonable to postulate that such changes in concentration of dissolved substances would have a greater relative effect at temperatures near 4°C than at much higher temperatures, such as 24°C.

The movements of water masses and the irregular isotherms in a small, ice-covered lake (Fig. 4) serve to emphasize the errors inherent in making deductions for an entire lake based on a series of observations at a single station.

From the data presented in Figure 4, it is obvious that on January 12 the water at 5.0°C was confined to the surface area over the deepest part of the lake and that there was a general decrease in temperature toward the upper, shallow end. By January 14, that 5.0-degree water was constricted to a small area about a meter below the surface over the deep water, but much of the other water mass had become slightly warmer, and the decrease in temperature toward the upper end of the lake was not so pronounced. Four days later only a small portion of the entire lake was cooler than 5.0°C, and the only large mass of cooler water was in the extreme east end of the lake in the same general area that had been occupied by the warmest water on January 12. In the east end of the lake, the vertical profiles showed a shallow lens of 4.9-degree water at the surface which was nearly separated from a much larger volume of water of the same temperature below it. This larger volume was almost surrounded with water of at least 5.0°C.

The temperature profiles through the longitudinal section of the lake (Fig. 4) show clearly that there was a distinct warming of the entire water mass from January 12 to 14, and from January 14 to 18. However, the mean temperature of the water column at the regular sampling station (Figs. 1 and 2) rose from 4.74°C on January 12 to 4.84°C on January 14, and fell to 4.80°C on January 18. Therefore, the heat budgets calculated from temperatures at one station are erroneous because the mass movement of warm water away from that station gave the false impression of a cooling period. Furthermore, the longitudinal series of profiles revealed that thermal gradients at different depths were extremely varied throughout the lake.

Because of local topography, some parts of the lake were not exposed to direct solar radiation. The longitudinal profiles (Fig. 4) were made along a transect extending from the west end of the lake between the two inlets (Figs. 1 and 5) to the center of the concrete standpipe in the deep water about 50 feet west of the dam. About half the temperature series was taken under constantly shaded ice, the other half under ice that was in a position to be exposed to direct sunlight. Thus, on January 12 and 14 the warmest water was under ice that had been exposed to direct sunlight for several days (Fig. 2), and the coldest water was under ice that had been in constant shade. On January 18 much of the warmest water was under ice that had not been exposed to direct sunlight, and the coldest water was under ice where direct solar radiation could have been a factor in heating the water. However, the sky was completely overcast from January 14 through 17, and the warming effects of the sun must be discounted for those days. It appears obvious that the coldest water moved to the deepest part of the lake and that the warmer

TABLE 3. *Mean temperature gradients ($d\theta/dz$) expressed as temperature changes per cm, Tom Wallace Lake, Jefferson County, Kentucky, 1958*

Arrows show direction of heat flow

Stratum m	Warming period Jan. 5–19	Cooling period (some open water) Jan. 19–Feb. 4	Warming period Feb. 4–16	Cooling period Feb. 16–21	Warming period Feb. 21–23
0–0.25	↓	none	0.105 ↑	0.0708 ↑	↑ 0.218
0.25–0.5	↓	none	0.0253	0.065	0.002
0.5–1	↓	none	0.0047	0.0135	0.011
1–2	↓	none	0.00016	0.0015	0.0065 ↓
2–3	↓	none	none	0.000125	none
3–4	↓	none	0.0005 ↑	0.000075	none
4–5	none	0.00015 ↑	0.00044	none	none
5–6	none	0.0001	0.0005	none	none
6–7	0.0005 ↑	0.0005	0.0012	0.00043 ↑	0.00215 ↑
7–8	0.0026	0.00085	0.0017	0.00265	0.0025
8–mud[1]	0.0183	0.00775	0.0073	0.0077	0.00625

[1] Until January 19, 8.3 m; after January 19, 8.6 m.

water spread out over the shallow parts. Still, it is difficult to explain from the data at hand why the coldest water on January 18 should have occupied virtually the same area that was occupied by the warmest water on January 12, or why much of that cold water was nearly surrounded by warmer water. Similar phenomena were manifest in the several profiles taken in transverse sections both in deep and in shallow sections of the lake, the data for which are not presented here. In those transverse sections, the movement of isotherms was from the sunny region toward the shade in a north-to-south direction.

It is obvious that the mechanisms involved in the rapid warming and cooling of the lake were complex and varied. However, by assuming that vertical thermal gradients showed the direction of heat movement, a few definite statements concerning heat transport can be made. The mean vertical gradients, $d\theta/dz$, expressed as temperature change per centimeter are presented in Table 3.

On all sampling dates, the thermal gradient from the mud to the overlying water suggested an upward movement of heat. During the first warming period (January 5 to 19), the temperature gradient extended up as far as the 6-m depth on three sampling days, and only to the 7-m depth on five days. No thermal gradients from 6 m to 5 m nor from 5 m to 4 m were noted, but the fact that thermal gradients were not uniform throughout the lake is clearly illustrated in Figure 4. Many temperature profiles over transverse sections of the lake were made also, and they emphasized even more clearly the irregular nature of the isotherms.

During the warming period of February 4 to 16, the thermal gradient extended from the mud up to the 3-m depth on two occasions. The mean values of $d\theta/dz$ during those days are shown in Table 3. From 3 m to 2 m, $d\theta/dz$ was zero.

During the cooling period from February 16 through 21, there was still evidence of the upward transport of heat from the bottom. There was a gradient from the mud to the 6-m depth, but from 6 m to 5 m and from 5 m to 4 m $d\theta/dz$ was zero.

From February 21 through 23, the bottom mud, the 8-m water, and the 7-m water lost heat, although there was a net gain in the entire water column. However, the lower temperature gradient was very similar to every other period beneath the ice; there was a decline from the mud upwards.

During the period from January 19 to February 4, the first ice cover disappeared slowly, and a second one appeared on the latter date. That was a time of heat loss, and of at least partial circulation. In open water, the values of $d\theta/dz$ were zero from the surface to 4 m because of wind action. From 4 m down, the inverse thermal gradient prevailed, although heat was lost at all levels, including the mud.

The vertical temperature profiles beneath the ice when the lake was partially open were quite different from those at the open station where wind had thoroughly mixed the upper four meters of water. Profiles were recorded underneath the ice near its edge, and then the boat was used to break through the ice to a station about 10 m away from the open water. Temperatures at comparable depths were somewhat higher under the ice away from the open water than at the edge of the ice or in open water. In addition, there was an almost uninterrupted inverse thermal gradient from the mud to the ice. This was especially marked on January 29, when at both stations beneath the ice, the gradient was interrupted only between 2 m and 1 m, where temperatures were identical.

From these data it would appear that the bottom sediments were a source of heat to the overlying water. However, we do not believe that we were seeing the classical picture of a great mass of sediment slowly releasing heat acquired during the summer and autumnal circulation, when hypolimnion temperatures are highest. In Tom Wallace Lake, the soft, profundal sediments overlying the original basin are only about 7 or 8 cm thick, and the rate and direction of all temperature changes occurring beneath the ice covers were about the same for the deep bottom deposits and the 8-m water (Table 4). The mean fluctuations in temperatures amounted to 0.128°C per day in the mud, and at 8 m the rate was 0.132° C per day. When the data from periods when the lake was open or semi-open are included, the fluctuations in temperatures of the sediment are even more similar to those of the overlying water—0.121°C per day in the mud, and 0.122°C at 8 m. Those data do not suggest a sediment of great thermal capacity, but rather a thin layer which was rapidly warmed and cooled. The reason for the persistent thermal gradient from the sediments upward may have been caused by warm density currents, derived at least in part from subsurface seepage, rather than to the slow release of summer heat from the bottom deposits.

The direction of heat flow at the surface under the ice varied much more than at the bottom of the lake. During the first warming period, the effects of solar radiation were obvious on January 9, 12, and 19. Then, the thermal gradients suggested heat moving downward from the ice to 2 m, 3 m, and 4 m, respectively. On January 14, following a day of warm rain and melting, the gradient was reversed, and heat seemed to be moving from the upper meter of water to the ice. The directions and extent of heat flow on these days are indicated by arrows in Table 3.

TABLE 4. *Mean rates of variations in heat and temperature beneath the ice, Tom Wallace Lake, Jefferson County, Kentucky, January–February 1958*

Depth m	Mean variations in degrees C per day	g-cal × 10^6 involved per day	g-cal/cm²/day for each stratum
0–1	0.251	5,386	23.0
1–2	0.191	3,435	17.6
2–3	0.116	1,737	10.6
3–4	0.119	1,461	10.8
4–5	0.110	1,075	9.7
5–6	0.081	583	6.8
6–7	0.086	400	6.7
7–8	0.112	234	6.8
8–8.75	0.132	30	3.1
Mud	0.128	—	—

From February 4 to 16 when the entire lake, including the upper meter, gained heat, the rise in temperature was on the order of 1.5°C at all levels. However, on each of the five days we sampled the lake during that period, the temperature gradient suggested heat leaving the lake through the ice.

The cooling period which followed, and extended through February 21, was characterized by another thermal gradient indicating upward transport of heat to the ice. On February 17, the temperature gradient started between 4 and 3 m below the ice, and at the same time, the transfer of heat from the bottom sediments upward extended only as far as the 6-m level. The value of $d\theta/dz$ was zero at both 6 m to 5 m, and 5 m to 4 m.

A short warming period occurred between February 21 and 23 before the ice became unsafe for sampling. On February 21, the

thermal gradient at the surface indicated the upward movement of heat from the first meter of water only, the mean value of $d\theta/dz$ there being 0.0422° C (Table 3). On February 23, a warm and sunny day, the thermal gradient was reversed, and heat seemed to be flowing from the ice down to a depth of 2 m.

So far, the discussion has dealt only with vertical heat flow. It is not known how much horizontal movement of heat was involved in warming the lake at the upper and lower levels. On the other hand, our data may indicate that heating at median levels was due to lateral movements on several occasions. From January 5 to 19, the mean temperature fluctuations at 5 m amounted to 0.088°C per day, and the net increase there was 0.75°C. However, on no day was there a vertical temperature gradient at 5 m. Furthermore, the mean vertical gradients at 4 m and 3 m were so slight that the temperature increases there must have been due largely to the lateral transport of heat. During the heating period of February 4 to 16, the vertical gradient at 2 m was zero, although that stratum gained heat at the mean rate of 0.161° C per day. Horizontal transport of heat must have been responsible for that warming also. In the days that followed, until February 21, the lake cooled under the ice. The values of $d\theta/dz$ were zero from 6 m to 5 m, from 5 m to 4 m, and were very low from 4 m up to 2 m. However, the temperatures at all those levels fell at the mean rate of 0.074° C per day during that period. The values of $d\theta/dz$ in the 2-m to 3-m, 3-m to 4-m, and 4-m to 5-m strata were zero during the last, short warming period. Still, the temperatures there rose at the rate of 0.023° C per day, except at 3 m where the rate was 0.045° C per day. Those increases must have been caused by horizontal rather than by vertical movements of heat. From these data it appears that most of the temperature changes at mid depths, and especially at 5 m, were caused by the lateral transport of heat. The longitudinal series of profiles (Fig. 4) and the many transverse series that were made suggest, in some cases, tongue-like masses of isothermal water being thrust horizontally.

Although the data for determining A values (coefficients of eddy conductivity) at various depths are available, such values are probably not significant. The upper two meters of water below the ice were influenced a great deal by direct solar radiation, and by loss of heat at the ice surface. Between 2 m and 6 m, vertical eddy transport probably was not so important as lateral transport of heat, especially for the 5-m level. However, there may have been displacement of water from the mud surface upward which might be considered vertical eddy turbulence. By using the formula,

$$A_z = -d\theta_{bz}/dt \cdot dz/d\theta_z$$

mean A values for the warming periods beneath the ice during January, and the first warming period of February were calculated to be: mud to 8 m, 0.33×10^{-2} g/cm/sec; 8 m to 7 m, 3.24×10^{-2} g/cm/sec; and 7 m to 6 m, 13.3×10^{-2} g/cm/sec. This reveals the A values to be far from constant even over very small vertical ranges, and certainly the magnitude at the 6-m depth reflects disturbance by horizontal movement of heat. During certain spans of time, the upper meter or two showed reversing thermal gradients from day to day, or showed an inverse gradient while the lake was gaining heat. At the bottom of the lake, the direction of the temperature gradient was uniform, but the water gained as well as lost heat while the gradient remained unchanged in direction. Thus, the calculation of A values from our data does not seem useful.

We have presented some data (Table 4) which show the rates of all variations of temperature at various levels while ice covered the lake. The greatest variation was in the upper two meters below the ice. Probably, much of this was caused by turbulence due to changing water densities at times of freezing and melting, and perhaps during rainfall. Also, the effect of direct solar radiation, caloric exchange during freezing and melting, and the loss of heat at the ice surface during cold days are shown

here. The temperatures of the mud, and those of the 8-m water fluctuated more than those of the overlying water up to 2 m, and temperature changes were at a minimum between 5 m and 7 m. Profile-bound density currents from subsurface seepage, and from sediment-derived solutes, or even possibly from the inlets could have been responsible for the fluctuating nature of the temperatures at 8 m and in the mud. When the data are considered as total calorie changes, or as calories per cm^2 of the area at each depth, the region of minimum variation is less clearly marked (Table 4).

STABILITY

On several occasions, the vertical temperature profile from the surface to the deepest part of the lake could not be reconciled with the density of water as a function of the prevailing temperatures. Chemical data, when available, were used to adjust densities. Density due to bicarbonate was added in the amount of 18×10^{-7} per mg/liter following the findings of Hutchinson (1941). Those additions explained the vertical temperature profile at times. On other occasions, it appeared that total solids and/or total iron might have accounted for apparent instability based on temperature alone. However, there were five occasions when the 8-m water appeared to have too little density based on temperature alone, and it could not be corrected with the available chemical data. The same was true on two occasions for the water at 4 m. It is possible that a temporary instability was encountered in each of those instances, although inaccuracies resulting in underestimation of total solids may have brought about the appearance of anomalous instability.

Some relative-density determinations were made on freshly collected lake water, using a Westphal balance. The results (Table 5) show that the observed densities could be reconciled with the temperature profile, even though the latter appeared anomalous. On another occasion, densities were determined of water that had been stored in a refrigerator for 11 days. In that instance, the experimental densities could not be reconciled with the stratification at the time of collection.

TABLE 5. *Actual and theoretical densities of water from different depths at different temperatures, Tom Wallace Lake, Jefferson County, Kentucky, January–February 1958*

All temperatures are in degrees C.

Depth m	Temperature in lake	Theoretical density	Experimental temperature	Theoretical density	Actual relative density
0	2.4	0.9999796	3.5	0.9999981	0.9997
4	4.85	0.9999942	4.9	0.9999934	0.9999+
8	5.1	0.9999902	5.1	0.9999902	1.0003

DISSOLVED OXYGEN

On January 5, very soon after the ice first prevented wind-driven circulation, the dissolved oxygen at depths of 0, 4, and 8 m was very much the same (Fig. 3). The water at the upper two levels was at about 90 per cent of saturation, and the 8-m water was at about 88 per cent. Within the next 5½ days, the oxygen at 8 m decreased at the mean rate of 0.6 mg/liter/day to a level of about 63 per cent of saturation, while the oxygen content of the upper waters fluctuated but remained high. The relative areal deficit for the water between 8 m and 8.5 m was about 0.013 mg/liter/day. During that period, the profundal sediments gained heat at a rate of 0.1° C per day. The heat gain and oxygen loss might be explained on the basis of warm density currents, originating to some extent as seepage, moving down the basin to deep water. The uptake of oxygen by bottom sediments below 8 m may have occurred also.

It is not known how far above 8 m the zone of lowered oxygen extended, but an upward displacement of water by density currents moving into the deepest levels of the lake could be expected. The oxygen at 4 m was significantly greater than that at 8 m except on two occasions, and no complete oxygen analyses at all levels were made until February 21, toward the end of the study. There had been a decline in oxygen at 8 m between February 15 and 21 under a cover of ice and snow. It represented a decrease in oxygen at the rate of 0.57 mg/liter/day,

and, again, a relative areal deficit of 0.013 mg/cm²/day. The 8-m water contained 7.8 mg/liter, about 63 per cent of saturation. However, the water at 7 m contained 11.9 mg/liter of dissolved oxygen, almost 95 per cent of saturation. Oxygen at all levels above 7 m was about the same, and ranged from 11.7 to 12.4 mg/liter. Thus, there was no evidence of extensive upward displacement of poorly oxygenated water on February 21.

On January 12, there was a sudden, marked decrease in the oxygen content of the 0-m and 4-m water for which there is no obvious explanation. It followed a warm period when there was a conspicuous ice melt. However, there was no snow on the surrounding hills to contribute melt water with oxygen-consuming soil compounds to the lake.

TOTAL ALKALINITY

Total-alkalinity values at depths of 0, 4, and 8 m are shown in Figure 3. Fluctuations were most conspicuous in the water at 0 m, either just below the ice or at the surface during brief periods of open water at the sampling station. The mean of the alkalinity at 0 m was 30.1 mg/liter, with a standard deviation of 5.9; at 4 m, the mean was 33.6 mg/liter with a standard deviation of 4.1; and at 8 m, the mean was 34.2 mg/liter with a standard deviation of 2.3.

Melting, freezing, and rainfall were responsible for the conspicuous variations in surface-water alkalinity. A decrease of 12.4 mg/liter in the alkalinity value from January 11 to 12 reflected dilution from melt water. It followed a sunny period when the mean air temperature for three consecutive days was the highest of the entire sampling period. Melted ice from the lake had a total alkalinity of only 3.2 mg/liter, a dilution on the order of 10 times that of the underlying water.

On January 14, the lowest alkalinity value recorded, 14 mg/liter, followed a day of steady rain during which minimum air temperatures did not fall to freezing. On that day the ice was covered with water and was so spongy that it would hardly support a man's weight.

When the ice cover was incomplete, and some circulation was possible, the diluting effects of rain and melting were not obvious in surface waters. Moreover, the days of prolonged solar radiation during mid-February were accompanied by extremely low air temperatures and a snow cover, and, as a result, no melting or dilution was evident. Toward the last of February the air temperatures rose, and the ice disappeared quickly. On February 26, when the ice was unsafe to walk on, the water flowing over the spillway had an alkalinity of only 28 mg/liter. That was the lowest value recorded at the lake's outlet, and must have been caused by dilute melt water.

A freezing-out effect may have been seen on certain occasions when the water immediately below the ice had a higher total alkalinity than the water at 8 m. The only times surface-water alkalinity exceeded that at 8 m followed periods when the maximum air temperatures did not rise to 0° C, and during which the ice increased in thickness.

Although the mean alkalinity at a depth of 8 m was higher and more nearly constant than that of the overlying waters, the fluctuations at that depth were, nevertheless, surprising. There was no steady, uninterrupted increase in bicarbonate content of the 8-m water during periods of stagnation, and on some occasions that water had a lower alkalinity than waters of the 0-m and 4-m levels. There may have been a correlation between the dissolved oxygen at the 8-m depth and the total alkalinity there; at least some increases in alkalinity coincided with decreases in oxygen, and some decreases in alkalinity coincided with increases in oxygen. In some instances those increases in alkalinity may have been caused by diffusion of bicarbonates from the deep sediments when oxygen deficits were the greatest. When the temperature of the water at 8 m, and that of the mud about 0.5 m below, increased, the increase coincided with bicarbonate increases at 8 m in only about half the instances. Therefore, if the gain at those levels was caused by warm density currents flowing down the basin slopes, the solutes that imparted density were not primarily bicarbonate.

Throughout the study period, the brook

TABLE 6. *Comparison of total iron and readily assayed ferric iron in filtered and unfiltered water from three depths, Tom Wallace Lake, Jefferson County, Kentucky, February 21, 1958*

Depth m		Unfiltered water		Filtered water		
				Filtrate		Residue
		Total iron	Ferric iron	Ferric iron	Total minus ferric iron	Total iron
0	mg/liter	0.6750	0.025	0.025	0.4063	0.2437
	% of total	100	3.7	3.7	60.1	36.1
4	mg/liter	0.5888	0.025	0.025	0.5375	0.0263
	% of total	100	4.2	4.2	91.3	4.5
8	mg/liter	0.7995	0.300	0.300	0.2775	0.2220
	% of total	100	37.5	37.5	34.7	27.8

inlet was pouring water into the lake at the rate of about 430 m^3/day. The mean alkalinity of the entering water was 22.9 mg/liter with a standard deviation of 2.5. The average alkalinity of the lesser inlet was about 17.3 mg/liter. Water constantly left the lake via the spillway, and, therefore, some flushing, mixing, and dilution of the lake must have occurred. The mean alkalinity of the 0-m, 4-m, and 8-m water was lower during February than during January, if we omit the data from January 12 and 14 when the surface water was extremely dilute. The flushing of the lake continued well into April with a steady decline of bicarbonate alkalinity. On April 4, water in the upper meter had an alkalinity of 28 mg/liter, and the brook inlet had a bicarbonate content of 27 mg/liter.

IRON

Several determinations were made of total iron in water from depths of 0, 4, and 8 m during the period from January 8 to February 21, inclusive (Fig. 3). The graphic values apply to iron in unfiltered water, and the mean results were: 0.5616 mg/liter at the surface, 0.6177 mg/liter at 4 m, and 0.8620 mg/liter at 8 m.

On February 21, the last day chemical analyses were made, a series of iron determinations was performed to compare iron in unfiltered samples with samples filtered through smooth, white, qualitative Cenco filter paper (Table 6). Determinations for ferric iron according to the thiocyanate method described by Ellis *et al.* (1948: 72) revealed no difference between unfiltered and filtered water. Ferric iron was 3.7 per cent of total iron at the surface, 4.2 per cent at 4 m, and 37.5 per cent at 8 m. However, the values for total iron reflect obvious effects of filtering. The differences between the total iron content in unfiltered water and the total iron in the filtrates were especially marked at 0 m and 8 m. Thus, on February 21, the iron was present in significant amounts in some particulate form at the surface and in the 8-m water. Particulate iron was much less common at 4 m, but probably there was much colloidal iron and small particles with adsorbed iron present in all the filtrates.

The iron found by the total-iron method in filtrates exceeded that detectable by the ferric-iron method alone by 16 times at 0 m and by about 22 times at 4 m. However, at 8 m, the ferric iron in the filtrate was greater than the other forms detected by the total-iron method. According to Ellis *et al.* (1948), such differences should be interpreted as ferrous iron. No special care was taken to avoid agitation of the samples, and the excess of ferric iron in the 8-m water, when compared to values at 0 m and 4 m, may represent non-particulate ferrous iron converted to ferric iron by aeration. The samples were taken at the end of a two-week period of stagnation, when dissolved oxygen was lowest at 8 m. On the other hand, the oxygen was about 63 per cent of saturation at that time, and it hardly seems reasonable to assume that the redox potential at the surface was such that much ferrous iron was diffusing out into the water. Furthermore, at that time, phosphate was lowest at 8 m, a fact that does not suggest substances diffusing from a reduced mud surface. In the light of this, we are reluctant to theorize the

presence of ferrous iron in any significant amounts.

Two determinations of total iron in the brook inlet averaged 0.0788 mg/liter, and one determination on water from the lesser inlet revealed total iron in the amount of 0.075 mg/liter. Based on these limited data, and on our calculations of the rates of flow of the two inlets, iron was delivered to the lake by those sources at a rate of about 50 g/day. A sample taken from the brook inlet several weeks later, when acidified and treated with thiocyanate, appeared to have about 0.0250 mg/liter ferric iron. Perhaps, then, about 10 g/day of soluble ferric iron flowed into the lake in the brook water. If brook water could flow down the basin slope to the depression where the 8-m water lay, it would contribute an excess of ferric iron not found in overlying depths. Undoubtedly, another source of iron was seepage. In some places at the shallow margins of the lake, areas covered with gelatinous, rusty-colored masses could be seen under the ice. They disappeared when the ice melted and circulation occurred. The Rosewood Shale, which makes up a large part of the lake's drainage basin, contains many concretions of limonite.

Iron was lost continuously from the lake by overflow at the spillway. The mean content of total iron, from five determinations, in outlet water was 0.4944 mg/liter, as compared with a mean of 0.5616 in surface waters at the regular sampling stations.

The lowest value recorded for iron at 0 m was on January 14, when the diluting effects of rain and melt water were obvious. On that same date, the minimal values for total alkalinity and total solids at the surface were recorded. Although the iron in surface waters was usually less than at 4 m and 8 m, there were exceptions. On January 23, the vertical distribution of iron was very similar to that of total alkalinity. The 8-m and surface waters were very similar in iron content, and both were higher than the 4-m water. On February 11, iron, as well as total alkalinity, in surface waters was higher than at 4 m and 8 m. This may have been further evidence of a freezing-out effect. The total iron content of melted ice from the lake was only 0.0375 mg/liter. Iron data from 8 m are lacking for February 13, but once again surface water had more iron than 4-m water. On February 21, a freezing-out effect was noted again when surface-water iron surpassed that of 4 m for the third time, an excess of particulate iron at 0 m making the difference.

Most of the time the iron content of the 4-m water was intermediate between that at 0 m and 8 m. Four exceptions were mentioned above, and another was noted on February 15 under a complete ice and snow cover. At that time the iron stratification was like that of the total alkalinity, with 4-m water the highest, 8-m water intermediate, and surface water lowest.

Thus, there were only two occasions when the total iron was not greatest at 8 m, on February 11 and 15.

The samples from January 29 (Fig. 3) were taken when the collecting station had been free of ice for about a week, although the lake was still partially covered. On that date the iron stratification was more nearly uniform than at any other time.

The total iron for 8 m (2.025 mg/liter) on January 10 was very much higher than any other value obtained. This may have been caused by an experimental error of some kind, although total solids at that time were at the second highest level found at 8 m.

TOTAL SOLIDS

Estimates of total solids agree fairly well with other chemical and physical conditions at the lake. The lowest total solids were recorded from the surface waters on January 12 and 14, when rain and melting ice had diluted the upper layers. That was the period when values for alkalinity and iron were also at their lowest.

The freezing-out effect seen in the surface alkalinity and iron values for February 11, also were obvious in the total solids at that depth, when 367 mg/liter were found. There were about 30 mg/liter of solids pres-

ent in melted ice which was lower than any value from unfrozen lake water.

The mean values for total solids were 113.3, 108.2, and 117.6 mg/liter at 0, 4, and 8 m, respectively. If the questionable datum, 367 mg/liter for February 11 at the surface, is disregarded, the mean for surface water would become about 90 mg/liter, and the vertical stratification would be similar to those of iron and total alkalinity at identical depths.

The mean of five determinations of total solids leaving the lake at the spillway was 78.8 mg/liter. That was comparable to total iron at the spillway, where the mean value was less than in surface waters at the sampling station in the lake.

Two determinations were made of total solids in water from the brook inlet, and one in water from the lesser inlet. The mean of those three was 90.8 mg/liter with a standard deviation of 16. Thus, values of total solids in inlet waters, when compared with surface waters, were relatively higher than with either total alkalinity or total iron.

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Algal Productivity in Salt Marshes of Georgia[1]

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ABSTRACT

Gross primary production of algae in the intertidal marshes on the coast of Georgia was measured at various seasons. Measurements were also made of light, temperature, pH, depth of flooding at high tide, and sedimentary chlorophyll. Migration of the algae in the sediments was observed along creek borders.

Production during low tide is 150 mg C/m²/hr in winter and 20–30 mg C/m²/hr in summer. Production under water, during high tide is 200 mg C/m²/hr in August and drops to 50 mg in winter. A relation between the changes in production and the regime of light, temperature, and tides is postulated. Changes in production during high and low tide alternate so as to result in a nearly constant daily production throughout the year. The annual gross algal production is estimated to be 200 g C/m². Net production is not less than 90 per cent of gross production. Photosynthetic efficiency varied from 3 per cent to less than 0.1 per cent.

INTRODUCTION

Although there is much current interest in marine productivity, the possible role of the benthic microflora as producers has been largely overlooked. Their possible importance is suggested by Moul and Mason (1957) who compared cell counts and chlorophyll extracts from intertidal sediments. Amounts of chlorophyll and cell numbers were comparable to those found beneath a similar unit area of coastal waters. The suggestion that algae on tidal flats may be significant producers was also made by Nelson (1947), who observed bubbles of oxygen (*sic*) trapped in a mat of *Schizonema* on the tidal flats of Cape May, New Jersey. The present study is concerned with the productivity of the microscopic algae of intertidal salt marshes and with the environmental conditions that influence it.

Salt marshes support several populations of primary producers: higher plants (Chapman, 1954, 1959; Moul and Brown 1957), algae on and in the sediments (Hustedt 1955, Nielsen 1957, Moul 1959), and phytoplankton in the estuarine water. Much work has been done on phytoplankton production. The production of *Spartina alterniflora*, the dominant spermatophyte of Atlantic coast marshes, has been investigated by Smalley (1959). Because marshes make up about 75 per cent of the area of the estuaries on the coast of Georgia, the production of marsh plants is important in its contribution to the energy flow of estuarine populations.

Most of the measurements of production and associated factors were made in the marshes of the Duplin River, a tidal creek adjacent to Sapelo Island, Georgia. The Duplin River has no significant source of fresh water except rainfall on its marshes; it is not a river but an arm of the estuary of the Altamaha River. Some aspects of the hydrography of this marshy tidal creek have been discussed by Ragotzkie and Bryson (1955).

Much of the marsh of the Duplin River is soft and silty with little development of peat. Areas of this type are low and well drained with well-developed drainage creeks (Fig. 1). Along the larger tidal creeks are natural levees (cf. Miller and Egler 1950). A small part of the marsh is high and sandy with remnants of high ground (locally called hammocks) scattered over the marsh. The elevation of various parts of the marsh has been shown to influence the higher plant associations, and marshes have been divided

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FIG. 1. Aerial photograph of a portion of the marshes of the Duplin River, showing low marshes with well-developed drainage and prominent levees along larger creeks. The Duplin River is in the foreground. A hammock wooded with oak and pine is in the center. Distance across center of picture: 900 meters.

into zones based on the dominant higher plants (Chapman 1954, Hinde 1954, Kurz and Wagner 1957).

No detailed taxonomic study of the algae was made in connection with the measurements of photosynthesis. Occasional examinations revealed that the most abundant algae were pennate diatoms of many genera. Green flagellates were present, and a creeping *Euglena* sometimes formed green patches on the sediments. Dinoflagellates were found occasionally in low, wet sediments. Blue-green algae formed mats on the surface of the sediments, particularly in late winter and early spring.

The writer's interest in the role of algae in energy flow in the salt marsh originated from conversations and field work with Edwin T. Moul. Thanks are due him both for the initial stimulus and for a critical review of the manuscript. Thanks are also due H. T. Odum for his interest and suggestions during the work and for critically reviewing the manuscript. The sedimentary chlorophyll determinations were done with the assistance of Ralph Warner and H. S. Robarts.

MATERIALS AND METHODS

Bell jars made from one-gallon bottles (Fig. 2) equipped with three-hole stoppers were pressed down into the sediments until the inlet tube nearly touched the surface. Sterile, filtered estuarine water (partially re-aerated) was slowly siphoned into each bell jar, without disturbing the sediment surface, and allowed to overflow until the bell jar had been flushed with twice its volume. Two D. O. bottles were filled with the water used for flushing, and from these the initial oxygen concentration was determined by the Winkler method (A. P. H. A. 1955). Because the water remained clear and free from suspended sediments, no special modification of the Winkler procedure was deemed necessary. A dial-type thermometer inserted through the stopper served as a stirring rod for gently mixing

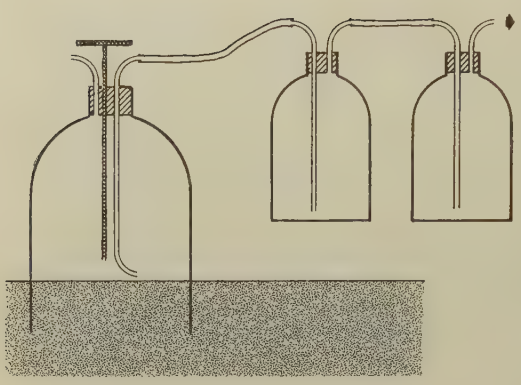

FIG. 2. Bell jar and bottle train used in estimating photosynthesis of algae under simulated high-tide conditions.

the water to prevent microstratification. After a period of exposure, usually one hour, the water in the bell jar was carefully siphoned out into two D. O. bottles, using a bottle train to flush the bottles. All oxygen samples were fixed at once in the field and titrated as soon as they could be taken to the laboratory. In the same manner dark bell jars were prepared and covered with a wooden box painted black inside. They were filled after all light was excluded.

If any of the water in a bell jar was lost through crab burrows or if bubbles rose from an unseen burrow during a period of observation, the bell jar was immediately emptied and the observation abandoned. A considerable number of observations were lost in this way, and the abundance of burrows in the marsh limited bell jar observations to the bare strand below the *Spartina* border.

The measurements of photosynthesis under bell jars were made at low tide on exposed sediment surfaces. Over a period of a year 43 measurements were made in this manner. By placing a photometer in the bottom of a filled bell jar it was found that as much light reached the sediment surface through the bell jar as through one-half meter of marsh water. The measurements therefore simulate photosynthesis during high tide.

A flowing-air system with CO_2-absorption columns (Verduin and Loomis 1944, Fig. 1) was used to measure photosynthesis during low tide. Air was drawn through lucite enclosures that were pressed into the marsh sediments. In order to avoid crab burrows and *Spartina* clumps two small enclosures (100 cm^2 each) were used in series. A flow rate of 25 liters per hour gave a significant change in the absorption columns after one hour without causing serious depletion of CO_2 in the measuring vessels. Usually on alternate hours throughout the day the enclosures were covered with black polyethylene film and aluminum foil to obtain respiration measurements. Three absorption columns were operated simultaneously, two drawing air through measuring vessels and one control drawing air from a point near the intake of the measuring vessels. At the start of each day all three columns were operated from a common air supply to check the reproducibility of results. The 95 per cent confidence limits of the method are ± 4 mg $C/m^2/hr$. Repeated observations in light or darkness revealed no evidence of lag, so it is assumed that the lag time is much less than one hour. Measurements were made during all daylight hours, and significant rates of photosynthesis were found soon after sunrise and through the late afternoon on sediments exposed to air. The mean rates given in this paper include approximately equal numbers of observations from all parts of the day.

Light was measured both in air and under water with a photometer built by L. V. Whitney. Light measurements were converted to energy units, assuming that 1.55×10^4 foot-candles equal one langley/minute (Jenkin 1937, Ryther 1956, Strickland 1958). All radiation measurements are given as photosynthetically active radiation, which is assumed to be half the total radiation. The use of a light meter as a means of measuring available energy undoubtedly introduces some error. The work of Blinks (1955) and others with algal action spectra suggests that the error is not a serious one in very shallow water. In some instances radiation was estimated from the tables of Kimball (1928).

The pH of the sediments was measured *in situ* with a Beckman model N pH meter. Surface pH was measured by lightly touching the electrodes to the surface of the sediments.

An attempt was made to estimate the

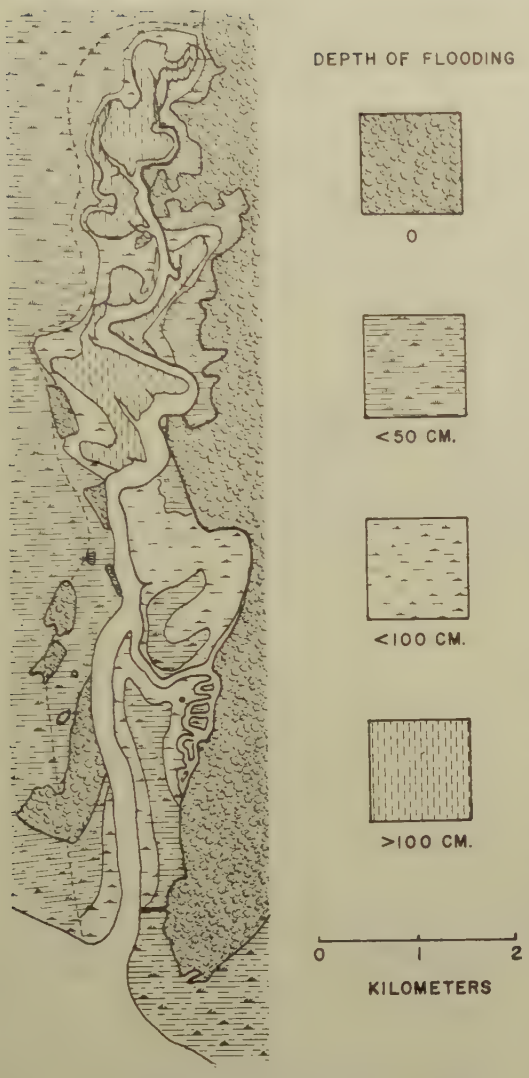

FIG. 3. Map of the Duplin River and its intertidal marshes. Contours represent depth of water at spring tide and are at high-water line, 50 cm below high water, 100 cm below high water, and 200 cm below high water (low water line). The 150-cm contour is omitted for clarity. Sapelo Island is on the right. The limit of drainage is shown by the dotted line. Outline of land and water areas from U. S. C. and G. S. Chart 574. Depths are from survey described in text.

standing crop of algae in the marsh sediments by means of pigment extractions. Marsh, lake, and marine sediments contain extracellular degradation products of plant pigments (pheophytins, pheophorbides, etc.) which have absorption spectra rather similar to those of the original pigments (Vallentyne 1955, Orr and Grady 1957, Orr *et al.* 1958). Therefore the pigment analyses used for phytoplankton are not suitable for work with sediments. The sedimentary chlorophyll method, a relative method developed for lake sediments by Vallentyne (1955), has been used in this work. It is not wholly satisfactory where there is a mixture of chlorophylls and their degradation products, because chlorophylls have a higher absorptivity than their degradation products (Orr and Grady 1957). This limitation should be kept in mind in interpreting the results of the pigment extractions. The term "sedimentary chlorophyll," originally used by Vallentyne (1955) to mean the degradation products of chlorophyll in sediments, is used in this paper to mean the relative concentration of chlorophylls and their degradation products in the sediments.

The depth of flooding of the marsh was determined by walking the marsh with a meter stick at high water. Five transects of the Duplin River marshes were traversed, and the depth of water was measured at intervals of 44 meters at 100 stations. Depths measured on different days were corrected by reference to a recording tide gauge at the mouth of the Duplin River. From the transect data a contour map of the Duplin River marshes was constructed (Fig. 3). From this the data in Table 1 were obtained by planimetry.

OBSERVATIONS

Temperature, pH, and light

Seasonal variations in daytime temperature of the air, water, and surface sediments are shown in Figure 4. The nighttime temperature of the sediments was found to approach the water temperature. Daytime temperature of the sediments was influenced by insolation, shading by *Spartina*, greenhouse effect of *Spartina*, and evaporation of water from the sediments. In winter the sediment temperature beneath dense stands of *Spartina* is lower than in bare areas. Presumably this is a shading effect. In summer the sediment temperature beneath dense *Spartina* is higher than on bare areas. This may be the result of a combination of greenhouse effect and reduced evaporation of

TABLE 1. *Morphometry of the marshes of the Duplin River, Sapelo Island, Georgia*

Depth at high tide cm	Area $m^2 \times 10^6$	Per cent of total area	Storage at spring high $m^3 \times 10^6$	Per cent of time exposed	Types of marsh
>100	2.1	22	2.1	<40	Bare strand, bare interior, tall-*Spartina* areas
100–50	3.6	36	1.8	60	Levee slopes, med.-*Spartina* areas
50–0	4.1	42	1.0	>75	Levee tops, *Salicornia* flats, short-*Spartina* and *Juncus* areas

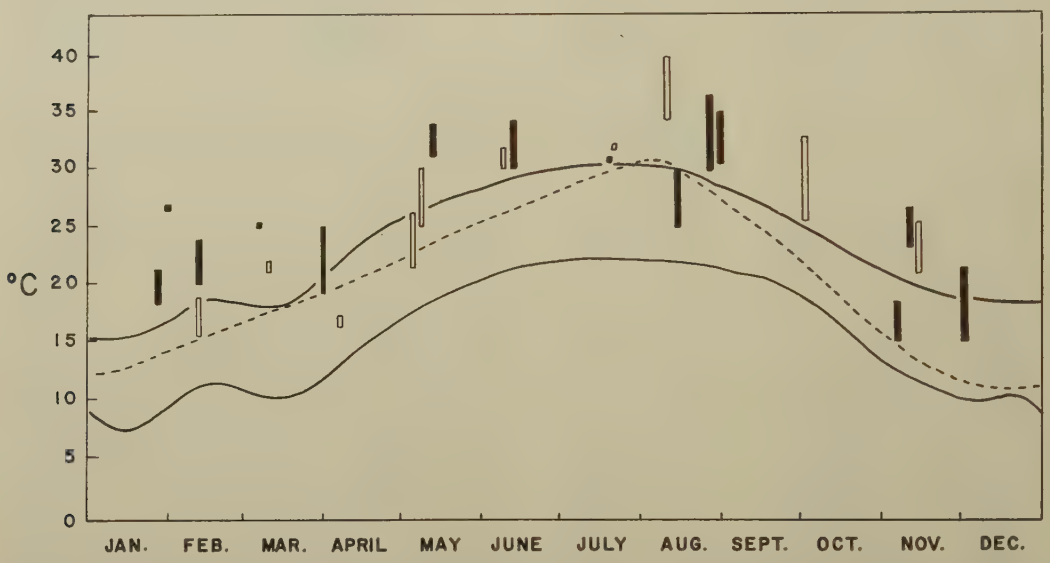

FIG. 4. Seasonal variations in temperature in salt marshes near Sapelo Island, Georgia. *Solid vertical bars:* observed daytime temperature range of surface of bare sediments. *Open vertical bars:* observed daytime temperature range of surface sediments under tall *Spartina*. *Broken line:* water temperature at mouth of Duplin River. *Solid lines:* maximum and minimum air temperature at Sapelo Island (Monthly means for 1956–7. Jan. 1956–April 1957 recorded by author; April–Dec. 1957 from U. S. Weather Bureau 1957.).

water from the sediments. On bare areas cracks appear in the sediments after several hours exposure, indicating considerable evaporation. Beneath *Spartina* the cracking is absent or greatly reduced. It is evident from Figure 4 that throughout the year sediment surface temperature tends to be higher than air or water temperature.

In the early morning, before the sun has risen, the pH of the marsh surface is between 7 and 8. During the day, when the marsh is exposed at low tide, the pH rises to 8.5 or 9 and occasionally to 10. Typical diurnal variation in pH is shown in Figure 5. The high daytime pH at the surface of the sediments influences the pH of the sediments to a depth of several centimeters.

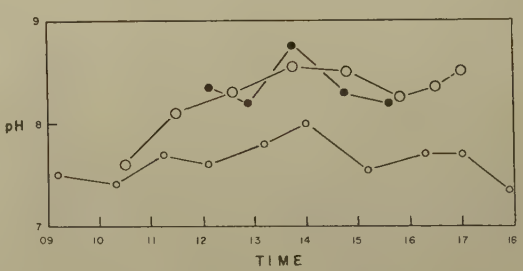

FIG. 5. Diurnal variations in pH of the surface of the sediments of the salt marsh, south end of Sapelo Island, May 10, 1956. *Small open circles*: station in sparse, 0.3-meter *Spartina* well back in marsh. *Large open circles*: station in dense, 1-meter *Spartina* on front of natural levee. *Black dots*: station on bare strand. All were observed from first exposure by ebbing tide to covering by flood tide.

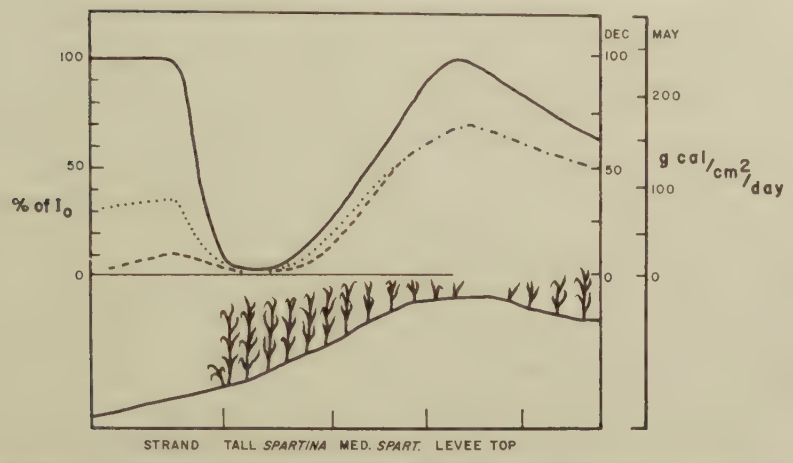

FIG. 6. Per cent of incident light reaching surface of sediments in different zones of marsh of Duplin River as measured with a photometer. *Solid line:* sediments exposed to air and full sun. *Dotted line:* sediments at mean depth of water for the period of flooding. *Dashed line:* sediments at maximum depth at high water. Scales at right give estimated maximum and minimum daily insolation for day of average cloudiness (based on Kimball 1928, Table 4).

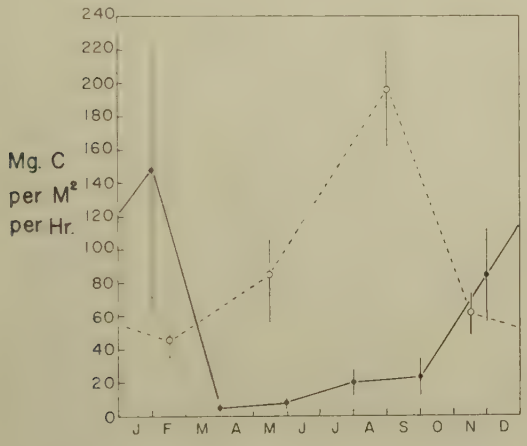

FIG. 7. Seasonal variation in gross algal production. *Black dots*: two-month means of rates at low tide. *Open circles*: three-month means of rates in simulated high tide conditions (bell jars). *Vertical bars* represent 95 per cent confidence limits of the means.

The amount of radiation reaching the algal flora of the marsh sediments varies not only with season and cloud cover but also with the density of *Spartina*, the depth of water during high tide, the turbidity of the water, and the depth of the algae in the sediments. The data in Figure 6 are expressed as vertical transmission, measured as vertical illumination (Hutchinson 1957, pages 389–424).

The turbidity of water in the major creeks draining the marsh, such as the Duplin River, is such that essentially all the light is absorbed in the first few decimeters. In the interior of the marsh the water in the smaller creeks and over the marsh proper is relatively clear and permits photosynthesis down to a depth of a meter or more. The extinction coefficient of water in the marsh and small creeks is 1.

Vertical migration

The vertical migration of diatoms in intertidal sediments has been observed by Aleem (1949), Fauré-Fremiet (1951), Callame and Debyser (1954), and others cited by them. Observations during the present study confirmed earlier reports, including that of Callame and Debyser that the diatoms will complete their downward migration just before the return of the tide even if the sediments are in the laboratory for study.

Certain aspects of migration are important in the interpretation of the effect of light intensity on algal production. Migration is limited to soft, wet sediments of the lower intertidal zone. In the marsh proper most algae remain at the surface at all times. In the bare sediments below the *Spartina* border the algae rise to the surface soon after the sediments are exposed by the

falling tide. Microscopic examination of undisturbed sediments and of 40-micron frozen sections of sediments indicates that at low tide all the algae are at the surface, usually forming a layer only one cell thick and seldom more than 5 cells thick. The depth of their vertical migration appears to be only a few microns in most cases. Therefore, at low tide the algae are all exposed to full illumination, while at high tide illumination is reduced by the overlying water and by a thin layer of sediments. A few algae are quite deep in the sediments (cf. Moul and Mason 1957), but these are probably unimportant as producers. It is important to note that the algae do not seek optimal light. Instead they seek full illumination, even though it may inhibit photosynthesis.

Rates of photosynthesis and respiration

Mean rates of gross algal production, based on measurements made at all times of day and under varying amounts of cloud cover, are shown in Figure 7. Photosynthesis during low tide is significantly higher in winter, while photosynthesis at high tide is significantly higher in late summer. The two complement each other in such a way that the rate of production over a tidal cycle will be almost the same throughout the year.

In calculating photosynthetic rates no correction was made for photosynthetic quotient ($Q_p = -dO_2/dCO_2$). Rabinowitch (1945, p. 31–35) reviewed experimental estimations of Q_p and concluded that it is not significantly different from 1.0 in most cases. Ryther (1956) on largely theoretical grounds suggested that 1.25 is more realistic, pro-

TABLE 2. *Gross algal production in various zones of the marsh of the Duplin River, mg C/m²/day*

Zone		Month					
		1–2	3–4	5–6	7–8	9–10	11–12
Bare strand	In air	+397	+3	+35	+78		+307
	In water	+415	+315	+777	+1541		+528
	Total	+812	+318	+812	+1619		+825
Tall *Spartina*	In air	+72	+12	0	+59	+120	+478
	In water	+275	+210	+518	+1027		+352
	Total	+347	+222	+518	+1086		+830
Medium *Spartina*	In air	−37	+120	+93	+17		+860
	In water	+183	+140	+346	+685		+234
	Total	+146	+260	+439	+702		+1094
Levee top	In air	+495		+52	+29		+228
	In water	+138	+105	+259	+513		+176
	Total	+633		+311	+542		+404

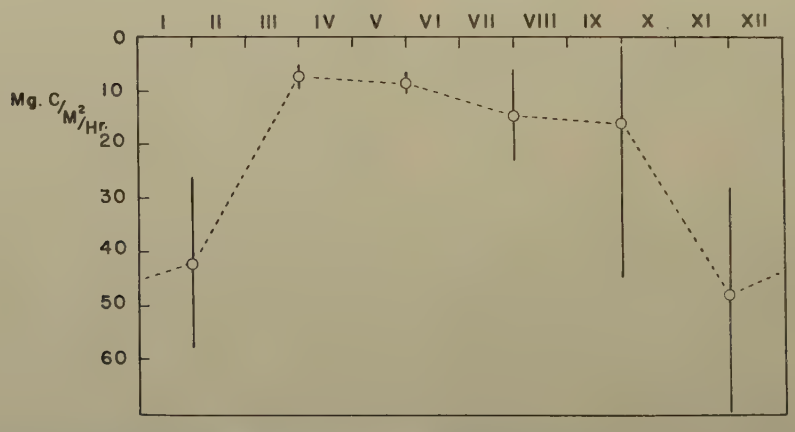

FIG. 8. Respiration in air of organisms in marsh sediments at various seasons. Each point is a two-month mean, with vertical bars representing 95 per cent confidence limits.

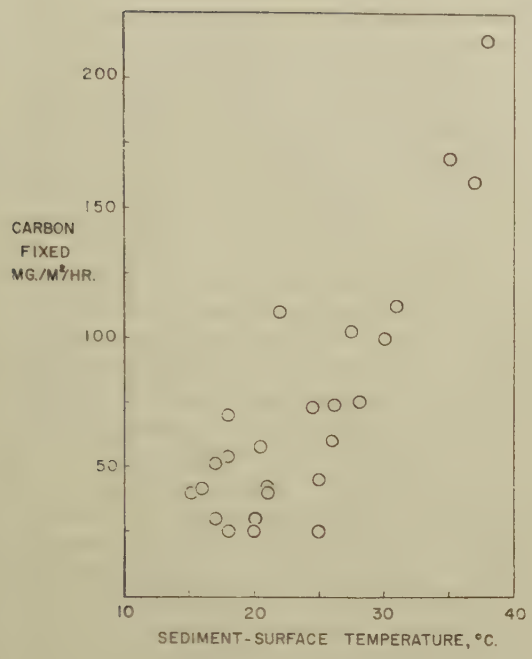

FIG. 9. Relation of photosynthesis to temperature in observations with water-filled bell jars simulating high-tide conditions.

vided the nitrogen source is nitrate. Where ammonia is the nitrogen source Q_p is expected to be nearer 1.0. It is possible that algae in marsh sediments may utilize ammonia to satisfy much of their nitrogen requirements.

Daily production was estimated from the short-term data by correcting for day length at different seasons and for the length of time each part of the marsh was inundated and exposed during a tidal cycle. The estimates in Table 2 are necessarily crude ones, for the number of measurements in individual zones of the marsh at different seasons is small. They should be taken only as a suggestion of the variety of conditions to be found in the marsh. The seasonal variations seen in the short-term data are still apparent, and the total production is smoothed.

From the daily production an estimate of annual production of algae in the Duplin River marshes was made by correcting for the relative amount of each marsh type in the study area (Table 1). Annual gross production was estimated to be 200 g C/m². For comparison a simple mean of all data was prepared, assuming production for six hours in air and six hours under water each day. This gave an estimate of 280 g C/m².

Measurements of community respiration were made in a ratio of about one for every two photosynthesis measurements. Under water the mean rate was 12.8 ± 2.9 mg C/m²/hr. No significant seasonal differences were found. Respiration when the marsh was exposed to air was significantly higher in winter (Fig. 8). This was surprising, and no explanation can be given. Several respiration measurements under bell jars for periods of 12 and 24 hours (the former at night) show mean hourly rates of about half the short-term measurements. This suggests that respiration is lower at night, although further data would be required to confirm this. The annual mean rate of respiration of the sediments community is estimated to be 100 g C/m².

To estimate net algal production it is necessary to separate the respiration of the algae from that of heterotrophic organisms of the sediments community. Because the algae are motile and migrate vertically, it is possible to select a time and place when all algae are on the surface of the sediments and to scrape them off almost quantitatively. The sediment exposed is well within the oxidized layer, and there is no reason to suspect great alteration of respiratory rate by the scraping process. After scraping, the CO_2 evolution of the scraped area is measured both in light and darkness to test the completeness of removal of autotrophic organisms. When all are removed the rate of CO_2 evolution is the same in both light and darkness. When such an area is compared with an adjacent undisturbed area, all respiration proves to be non-algal. On the basis of the estimated accuracy of the method there is a 95 per cent probability that net algal production is not less than 90 per cent of gross production.

Standing crop of algae

In the Georgia marshes there is a sharp reduction in sedimentary chlorophyll below the first centimeter of sediments and no further reduction down to one meter (the

TABLE 3. *Horizontal distribution of sedimentary chlorophyll in salt-marsh sediments, expressed as sedimentary chlorophyll units per gram dry weight of sediments*

Location	S. end Sapelo Island	Duplin River		Duplin River	
Date	8–28–57	9–3–57		10–7–57	
Depth	Surface	Surface	2 cm	Surface	2 cm
Bare strand		25.5	3.6	5.1	3.3
Tall *Spartina*	10.2	9.3	4.2	12.9	4.1
Med. *Spartina* levee front	8.6	4.5	2.5	10.7	3.6
Top of levee	4.4	2.5		5.0	1.7
Back of levee	4.9				
Short *Spartina*	6.0				
Med. *Spartina*	6.0				
Bank of interior creek	6.0				

deepest level sampled). Horizontally there are considerable variations in the sedimentary chlorophyll of the surface sediments (Table 3), and these give every evidence of following the pattern of standing crop as judged by the appearance of the marsh surface. Also, the most productive areas show the highest sedimentary chlorophyll values. However, other factors, such as the rate of sedimentation, could be involved (cf. Orr *et al.* 1958).

Visual observations through several years give some indication of the spatial and seasonal variation in standing crop. During the summer and early fall there is a dark brown zone on the bare strand of the lower intertidal zone. In winter this disappears almost completely, and the strand is a dull grey. In winter and spring a zone of blue-green algae develops on the upper part of the levee. Also in spring a rich brown color develops beneath the tall *Spartina*. The relation of these changes to the regime of the physical environment is suggested in the following section.

DISCUSSION

The rate of algal production in Georgia salt marshes is similar to the production of phytoplankton in many aquatic ecosystems (cf. Juday 1940, Lindemann 1942, Clarke 1946, Riley 1953 and 1955). When the total production of the marshes is estimated, including *Spartina* and phytoplankton as well as the algae of the sediments (Teal 1959), it will probably be comparable to the most productive aquatic and terrestrial ecosystems (Odum 1956 and 1957, Loomis 1949). Certainly the production of algae in salt marshes is a significant contribution to the energy flow of the ecosystem of marshy estuaries.

Of the factors that influence production, light is probably most important and best understood. The amount of light reaching the surface of the sediments at any time and place can be estimated from existing data (Fig. 5). During low tide, when the algae are exposed to full sunlight and are in a layer which is at most a few cells thick, the amount of light reaching the algae can be known accurately. During high tide the algae in lower, wetter sediments migrate downward (probably a very short distance), and part of the light is absorbed by the water and sediments before it reaches the algae. The absorption by the water can be estimated from Figure 5, but the absorption by the sediments cannot be estimated with any precision until more is known about the extent of the migration and the transparency of the sediments.

The effect of light intensity on photosynthesis by phytoplankton has been investigated by Ryther (1956), Talling (1957a and b), and Sorokin and Krauss (1958). A wide variety of species and higher taxa are represented by these experiments, and the results should be applicable to the algae in intertidal sediments, making allowance for the very limited vertical distribution of the sediment's algae. Ryther found that the optimal light intensity for photosynthesis was between 350 and 3000 foot-candles, depending somewhat on the major taxonomic group involved. Illumination above or below the optimal range inhibits photosynthesis (cf. Ryther 1956, Fig. 1). The observations of Talling and of Sorokin and Krauss confirm those of Ryther.

Photometric measurements in the salt marsh show that incident light exceeds the optimum during midday throughout the year, except on a few very cloudy days. However, in spring and early summer the

optimum is exceeded by 0800 hours, and light remains above optimum until 1600 or 1700. Therefore, during low tide light must be limiting much of the time, particularly in spring and summer. Since the algae are all at the surface and are not more than a few cells thick, light is limiting to essentially all of the population. Beneath *Spartina* illumination is nearer the optimum, although still above it except under the dense, tall stands along the levees. When the marsh is under water much of the sediment surface is within the optimal range of illumination in spring and summer and somewhat below it in fall and winter. Creek bottoms covered by more than two meters of water are probably at or below the compensation level.

With sub-optimal illumination photosynthesis is independent of temperature, but within the optimal range it is temperature-dependent (Rabinowitch 1956, p. 1211–1242; Talling 1957a). This being so, it may be expected that in the bell-jar observations photosynthesis is a function of temperature (Fig. 9). When light is above the optimum, photosynthesis is temperature dependent (Rabinowitch 1956, p. 1211). However, in the flowing-air observations, where light was often above the optimum, there is no apparent relation of photosynthesis to temperature, probably because the varying degrees of inhibition of photosynthesis by strong light mask the temperature effect.

From light and temperature relations it is possible to understand the seasonal changes in the rate of photosynthesis of marsh algae. In air light is limiting to photosynthesis, because it is too intense much of the time. In winter, when light is at its minimum, photosynthesis during low tide reaches its annual maximum. When the algae are under water light is in the optimal range much of the time, and the rate of photosynthesis reaches its maximum in August when water temperature is highest. Thus the interaction of light, temperature, and tidal regime appear to result in continuous production of algae.

The high pH of the marsh sediments during daylight suggests that CO_2 may be limiting at times. At a pH of 10 growth stops in cultures of *Nitzchia* and *Navicula* (Harvey 1955, p. 104), presumably because there is neither free CO_2 nor HCO_3 in the water. A pH of 10 was observed on several occasions.

It is possible to estimate approximately the diffusion rate of CO_2 across the sediment surface from the data given by Haney (1954) and Odum (1956). Bearing in mind that the algae are in constant motion, a net production rate of about 300 mg C/m^2/hr may be sustained by diffusion. This is in accord with the present observations, and it suggests that while availability of CO_2 is not the principal limiting factor it does impose an upper limit on productivity of algae in intertidal sediments. The advantages of flowing systems, which permit an increase in energy fixation in excess of the kinetic energy of the flowing water, have been pointed out by Odum (1956, 1957). In the marsh sediments flow (except tidal flow over the surface) is eliminated. The limitation imposed on production by the rate of diffusion of CO_2 into the surface layer of the sediments is far below the production rates that have been found in flowing systems (Odum 1957, Odum and Odum 1956).

The nutrient relationships of the algae in marsh sediments are not completely known. When algae migrate below the compensation depth in the sediments they may be living heterotrophically on dissolved organic materials in the interstitial water. Bristol-Roach (1928) found this to be the case with *Scenedesmus* living in soil. The algae are well situated to receive nutrients regenerated in the sediments, and inorganic nutrients are probably more abundant in the sediments than they are in the estuarine water. The high pH caused by photosynthesis of the algae may release nutrients from the sediments (Macpherson *et al.* 1958).

The efficiency of photosynthesis was calculated on the basis of photosynthetically active radiation reaching the surface of the sediments through the measuring vessels used. Efficiency is inversely related to light intensity, and is highest at the lowest intensities found under the range of conditions observed. Efficiencies of 1 to 3 per cent were found at light intensities less than 100 K Cal/m^2/hr, while at intensities in excess

of 300 K Cal efficiency was 0.1 per cent or less. The highest efficiencies were found in populations under water and under dense *Spartina* on the front of the natural levees. The low efficiencies observed are quite typical of algal populations (Steemann Nielsen 1957).

The long-term efficiency, computed on the basis of the annual estimate of gross algal production and Kimball's (1928) tables of average solar radiation (× 0.5) is 0.3 per cent. Since some of the energy is absorbed by *Spartina* or by water the true efficiency will be somewhat higher but probably less than 1 per cent.

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Trace Analysis of Marine Organisms: A Comparison of Activation Analysis and Conventional Methods[1]

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ABSTRACT

A comprehensive review has been made of the abundance values reported for all trace elements in seaweed, mollusks, crustaceans, fishes, and in sea water. The sensitivities of standard spectrophotometric and flame photometric techniques for such analyses have been compared with the sensitivities expected from activation analysis techniques.

Activation analysis eliminates the problem of contamination by reagents and is particularly useful for the analysis of minute traces. While it is not an "all purpose" method for every element, it does show promise of increasing the detection sensitivity for a number of elements by factors of 10, 100, or more as well as making possible the discovery of elements not previously found in marine organisms, such as elements of the ruthenium or platinum groups and indium.

INTRODUCTION

Studies of trace elements in biological materials were initially made by spectrographic analysis, augmented more recently by flame photometry. Concentration of these elements has been aided by solvent extraction with organic reagents and by ion-exchange. Nevertheless, the systematic knowledge of the abundance of trace elements in marine organisms is far from complete.

The most serious difficulty encountered in such analyses is contamination by minute quantities of the desired element which are present in the reagents used. The reliability of the results thereby tends to be lowered, even when carefully determined "reagent blank" values are subtracted.

The technique of radioactivation analysis is not limited by this consideration, since only the trace elements in the sample are activated (and subsequently measured). In activation analysis the constituents of a sample are determined by utilizing certain nuclear properties of the isotopes of the elements in the sample. Radioactive isotopes are formed by activation of the nuclei of the sample elements using nuclear particles. These radioisotopes formed can then be detected and measured by their nuclear radiations. Thus a knowledge of their nuclear characteristics allows a determination of the amount of element present.

This technique has been used for determination of submicrogram amounts of elements in semi-conductors (Jakovlev 1955, Smales 1955c), for measuring trace impurities in construction materials for nuclear reactors (Jenkins and Smales 1956), and in the field of geochemistry of minor elements (*e.g.*, Brown and Goldberg 1949, Goldberg and Brown 1950, Smales 1952, Smales 1955a, Smales and Salmon 1955, Vincent and Smales 1956). It has also been applied to the analysis of trace elements in biological materials (Loveridge and Smales 1957). Several review articles covering various aspects of this technique have also been published (Jenkins and Smales 1956, Meinke 1956, Meinke 1958, Meinke and Maddock 1957, Smales 1955b).

It should be kept in mind, however, that activation analysis is not an "all purpose" method for any element in any type of sample. A general comparison (Meinke 1955) of the sensitivity of activation method with that of other methods has already been made, in addition to more specific comparisons (Jenkins and Smales 1956, Schindewolf 1958). Such information should be valuable

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in determining which elements are suited to activation analysis in studies of trace elements in marine organisms.

In the present phase of this study it is important not only to describe the occurrence of elements in samples, but also to deduce the laws governing the distributions and variations of these elements. Here the radioactivation technique should prove to be a powerful tool.

In the following sections, a review of current values of the abundance of trace elements in marine organisms will be given. Consideration of the sensitivity of activation analysis for these elements is also included.

ABUNDANCE OF TRACE ELEMENTS IN MARINE BIOLOGICAL MATERIALS AND SEA WATER —LITERATURE SUMMARY

Table 1 gives the most reliable, up-to-date abundance values for trace elements in marine organisms and sea water, estimated on the basis of the data in the literature. Appropriately weighted data from two or more authors were cited when possible.

The four groups—seaweeds, mollusks, crustaceans, and fishes—were chosen as representatives of marine organisms, while sea water was added as the source of the elements contained in these marine organisms. It is admittedly sometimes difficult to obtain a representative value for a classification of this kind since each group includes a number of species, and since the abundance of some elements varies widely among species.

The significance of the table, therefore, is not to offer a basis for precise discussions, but only to generalize the abundance of trace elements in marine organisms preliminary to further detailed studies.

It is well known that the content of some elements in sea water varies considerably with the location of sample collection. For simplicity, values for the oceanic surface water have been given in the table. Although coastal waters should be the more important environment of organisms, variation in conditions makes it difficult to obtain representative values for these waters. It may be possible, however, to estimate an order of magnitude of content of coastal waters from that of the oceanic water.

All trace elements that have been mentioned in the literature on marine organisms are included in the table. Eleven elements, including hydrogen, carbon, nitrogen, oxygen, sodium, magnesium, phosphorus, sulfur, chlorine, potassium, and calcium have been excluded since they are major constituents of marine organisms. Lanthanide elements have been tabulated together since no reliable data on the separation and determination of each rare earth element have been reported.

Comments regarding each element included in Table 1 are given below. References on which these comments are based are listed in the table.

A. *Lithium to silicon*

Since elements that are primary components of biological materials were excluded, only six elements of this series remain.

Although at present only a few data have been reported for lithium, many more should be forthcoming since its sensitivity to the flame-photometric method is very high. Beryllium has been detected only qualitatively in the ash of seaweeds by spectrographic analysis.

Most of the data for fluorine are quite recent and show about equal concentrations in each group of organisms.

Despite the widespread occurrence of aluminum and silicon, reliable values for these elements are quite rare, probably because of easy contamination of the sample. Aluminum content tends to decrease with ascending trophic level.

B. *Scandium to zirconium*

These elements include most of the metals which appear to be important for the metabolism of marine organisms.

No direct determination of scandium has been made, although the estimated value for sea water has been given.

Titanium decreases with the ascending trophic level in a manner similar to aluminum, so that the ratio of aluminum to titanium remains constant in any group of

TABLE 1. *Occurrence of trace elements in marine organisms and sea water*
All references through 1957 are included. These are tabulated in columns labelled "Sources of data" by corresponding numbers in list of references. Figures in the columns *pA* are the negative logs of abundance (grams of element/grams dry weight at 105–110°C).

Atomic no.	Element	Seaweeds		Mollusks (without shell)		Crustaceans (without carapace)		Fishes (soft parts)		Sea water (in solution)	
		pA	Sources of data	pA	Sources of data	pA	Sources of data	pA	Sources of data	pA	Sources of data
3	Li	5.7	9, 12	6.0	27,111	−		+	109	7.0	103
4	Be	+	24, 58	−		−		−		−	
5	B	3.8	31, 42, 53, 81	4.3	31,111	4.3	31,111	5.0	31	5.35	42,109
9	F	5.0	109	5.3	66, 105	5.3	66, 105	5.3	22, 66, 105, 109	5.85	13
13	Al	4.2	30, 71, 114	4.3	72	4.7	72	5.3	71, 109	8.5	45, 90
14	Si	3.0	30, 109	(3.0)	109	(2.5)	108	3.5	101	6.3	1, 29
21	Sc	(6.0)	4	−		−		−		(10.4)	34
22	Ti	4.5	12, 30, 36	4.7	11, 49	5.0	11, 49	5.7	80	9.0	36, 80
23	V	5.7	4, 8, 12, 109	6.0	6, 8, 51	6.3	6, 8	6.7	6, 8, 80	9.5	12, 43, 54, 60, 80, 110
24	Cr	6.0	4, 12, 114	−		+	78	6.7	78, 80	10.3	12, 43, 54, 80
25	Mn	4.3	12, 30, 81	4.5	109	4.5	109, 111	4.7	80, 85	9.5	32, 38
26	Fe	3.1	12, 30	3.5	79	4.3	26, 79	4.3	79	8.5	23, 61, 90
27	Co	*6.3*	4, 12, 64, 96	6.3	64, 106	6.7	64, 106	6.7	64, 80, 106	10.0	12, 32, 43, 54, 60, 80
28	Ni	5.7	4, 12, 64, 114	6.0	64	6.3	64	6.3	64, 80	9.5	12, 32, 43, 54, 60, 80
29	Cu	5.1	4, 12, 81	4.3	7, 65, 79	4.5	7, 26, 79, 109	5.3	7, 16, 79	9.0	2, 20, 74
30	Zn	4.3	4, 12, 114	(3.5)	84, 109	(3.3)	84, 109	4.0	80	8.5	54, 74
31	Ga	(6.3)	4, 24, 109	−		−		7.0	80	7.5	19, 80
32	Ge	+	24, 58, 109	−		−		6.0	80	7.3	19, 80
33	As	4.5	35, 89, 113, 114	5.4	89	5.3	89, 109	5.2	80, 89	*8.5*	35, 43, 97
34	Se	−		−		−		−		(8.4)	34, 43, 110
35	Br	3.2	50, 77	(3.5)	77, 109	(4.0)	109	(5.3)	77	4.2	103, 109
37	Rb	*5.0*	10, 15, 98	5.0	27	−		−		*6.9*	15, 44, 98
38	Sr	*3.5*	14, 17, 99	*3.8*	17, 111	(3.7)	14	3.8	111	*5.1*	17, 21, 41, 91
39	Y	±	109	−		−		−		(9.5)	34
40	Zr	(5.5)	4	−		−		−		+	109
41	Nb	−		−		−		±	78	−	
42	Mo	6.3	4, 5, 12	5.7	7	6.3	7	6.3	7, 80	(9.3)	12, 43, 54, 60, 80, 110
47	Ag	6.5	4, 12, 114	+	27	+	27, 78	(5.0)	78, 80	9.7	12, 54, 80
48	Cd	6.2	63, 75	5.7	75, 104, 111	6.8	75, 104	(6.3)	80, 104	10.0	32, 54, 75, 80
50	Sn	6.0	4, 12, 114	(4.7)	111	(4.7)	111	5.5	80	8.5	12, 80
51	Sb	+	24, 58	−		−		6.7	80	>9.3	80
53	I	3.8	37	5.7	79	6.0	3, 26, 79, 109	5.7	79, 109	7.3	102, 103
55	Cs	*7.0*	98	−		−		−		*9.3*	44, 98
56	Ba	*5.3*	17	*6.5*	14, 17	(6.3)	111	+	78	*8.2*	17
57–71	Lanthanide Els.	+	4, 88	−		−		−		9.2	34
74	W	+	24, 58	−		−		−		10.0	43, 54
75	Re	±	46	−		−		−		−	
79	Au	(6.0)	4, 24	−		−		8.0	80	*10.5*	40, 82
80	Hg	7.5	83	−		−		(6.5)	83	10.5	34, 54
81	Tl	−		−		−		−		>11.0	32, 80
82	Pb	5.3	4, 12, 114	5.7	73, 109	6.0	73	6.5	80	8.3	12, 32, 54, 80
83	Bi	+	24, 46	−		−		7.5	80	9.7	54, 80
88	Ra	13.3	25, 28, 56, 112	−		13.3	25, 56	13.7	56	16.2	39, 52
90	Th	(6.0)	4	−		−		−		13.4	39, 52
92	U	+	24, 58	−		−		−		*8.7*	52, 76, 100

\+ element has only been detected.
− element has not been detected or reported.
± detection uncertain.
(□) less reliable values.
Figures in *italics* include results obtained by activation analysis.

organisms. However, the values used in the estimation of these representative values are somewhat dated.

Vanadium shows variations similar to aluminum and titanium. It is known, however, that this element is concentrated in certain species of mollusks. Since recent reported values for vanadium content in sea water seem to be high and since relatively large variations of vanadium content in coastal waters are likely to occur, the accumulation of more precise data is required.

Only a few values are available for chromium.

Although marine organisms contain a relatively large amount of manganese and iron, it was recently proven that the amount of these elements in true solution in sea water is extremely low and that they exist for the most part in particulate form (Goldberg 1954, Harvey 1949, Lewis and Goldberg 1954).

The fact that cobalt is concentrated relative to nickel in marine organisms is interesting, since Vitamin B_{12} is a cobalt-containing compound. Content of these two elements shows considerable variation from species to species.

Only a few of the many data reported for copper and zinc can be considered reliable since the older methods used have been shown to give high results. It is well known that copper is concentrated in the blood of mollusks and crustaceans, while zinc appears more highly concentrated in marine animals than in seaweed.

Although new information for gallium and germanium in sea water is available, the values seem rather high when compared with previous values.

Analyses of arsenic have been made by several methods including the radioactivation method for sea water. Only a value estimated from the content in sedimentary rocks is available for selenium.

Although bromine is relatively abundant in marine organisms as well as in sea water, the wide spread of reported values indicates considerable uncertainty about this element.

Activation analysis data for rubidium and strontium in sea water and in some groups of marine organisms have recently been published (Bowen 1956, Smales and Salmon 1955).

Reliable data are not available for yttrium and zirconium, although some values have been listed for purposes of reference.

C. *Niobium to barium*

These elements range from atomic number 41 to 56. Only nine of these elements have been inserted in the table. In the future, however, activation analysis should provide a sensitive method for additional elements such as ruthenium, rhodium, palladium, and indium.

Reports on niobium are limited to a possible detection in some fish.

Many values have been published for molybdenum, especially for its abundance in sea water. Reexamination of these data might reconcile discrepancies among individual values.

Since the value obtained for silver in fishes appears too high and since the analyses were done near the lower limit of detection, rechecks of the values are desirable.

Reliable data from cadmium have been supplied recently. It is interesting that radioactive cadmium (Cd^{113m}, Cd^{115m}) was found in the soft tissues of some fishes caught near Bikini Atoll (Unpublished data from Tokai Regional Fisheries Research Lab., Tokyo, Japan). This fact may suggest some physiological significance of cadmium in the metabolism of marine organisms.

Since a definite tendency towards concentration of tin is implied from the values in the table, more measurements should be made in the future to verify this idea.

Only a few data have been reported for antimony.

Iodine is the only element for which comprehensive studies have been carried out. A number of data have been accumulated for the occurrence and variation of this element in marine organisms. It is known that the content of iodine varies greatly from species to species and, therefore, the value quoted for each group of organisms represents only an average abundance.

Recently, reliable activation analysis data for cesium and barium in sea water as well as in marine organisms have indicated that

the abundance of these elements is less by a factor of 10 than that previously accepted (Bowen 1956, Smales and Salmon 1955). As for cesium, comprehensive studies have been planned in connection with radiocesium (Cs^{137}) contamination from radioactive fall-out.

D. *Lanthanum to uranium*

There are relatively few data for these elements except for some rather out-of-date values for lead and radium. The amount of gold and uranium in sea water has recently been determined by activation analysis. The gold content of coastal waters varies over a wide range.

It may be expected that data for the lanthanide elements will be supplied by application of the activation technique.

More work should be done on tungsten and rhenium.

TABLE 2. *Comparison of sensitivities of activation method with those of conventional methods for the elements present in marine samples*

Atomic No.	Element	Sensitivity of activation analysis				Sensitivity of conventional analysis		
		Mass No. of parent	Half-life of daughter	Sensitivity (g)	Sensitivity index	Sensitivity (g)	Sensitivity index	Method
21	Sc	45	**85d**	3×10^{-8}	7.5	4×10^{-7}	6.4	Morin
22	Ti	50	5.8m	5×10^{-6}	5.3	4×10^{-6}	5.4	Hydrogen peroxide
23	V	51	3.8m	6×10^{-8}	7.2	3×10^{-7}	6.5	Phosphotungstate
24	Cr	50	27d	1×10^{-5}	5.0	4×10^{-7}	6.4	Diphenylcarbazide
25	Mn	55	2.6h	1×10^{-10}	10.0	5×10^{-6}	5.3	Permanganate
26	Fe	58	45d	1×10^{-5}	5.0	1×10^{-5}	5.0	o-Phenanthroline
27	Co	59	*10.5m*	2.5×10^{-7}	6.6	5×10^{-7}	6.3	Nitroso-R salt
28	Ni	64	2.6h	1×10^{-7}	7.0	1×10^{-5}	5.0	Dimethylglyoxime
29	Cu	63	12.8h	5×10^{-9}	8.3	2×10^{-6}	5.7	Dithizone
30	Zn	68	**52m**	1×10^{-8}	8.0	2×10^{-6}	5.7	Dithizone
31	Ga	69, 71	21m, 14.1h	5×10^{-9}	8.3	1×10^{-7}	7.0	Fluorometric
32	Ge	74	82m	1×10^{-8}	8.0	1×10^{-5}	5.0	Heteropoly-molybdate
33	As*	75	26.6h	2×10^{-9}	8.7	5×10^{-6}	5.3	Heteropoly-molybdate
34	Se	80	18m	3×10^{-8}	7.5			
35	Br	79	*4.5h*, **18m**	2×10^{-9}	8.7			
37	Rb*	85, 87	18.6d, 17.8m	2.5×10^{-7}	6.6	4×10^{-7}	6.4	Flame-photometric
38	Sr*	86	2.8h	2×10^{-7}	6.7	4×10^{-7}	6.4	Flame-photometric
39	Y	89	64.2h	1.5×10^{-8}	7.8			
40	Zr	96	17h	1×10^{-6}	6.0	4×10^{-5}	4.4	Alizarin
41	Nb	93	6.6m	2.5×10^{-7}	6.6	2×10^{-5}	4.7	Quinalizarin
42	Mo	98, 100	67h, 14.6m	2.5×10^{-7}	6.6	2×10^{-6}	5.7	Thiocyanate-stannous chloride
47	Ag	107	2.3m	1×10^{-6}	6.0	1×10^{-6}	6.0	p-Dimethylaminobenzilidenerhodamine
48	Cd	116	2.9h	3×10^{-8}	7.5	1×10^{-7}	7.0	Dithizone
50	Sn	120, 122	27.5h, 4.0m	5×10^{-7}	6.3	2×10^{-5}	4.7	Dithiol
51	Sb	121	2.8d	1×10^{-8}	8.0	2×10^{-6}	5.7	Rodamine B
53	I	127	25m	1×10^{-9}	9.0			
55	Cs*	133	*3.2h*, **2.3y**	5×10^{-7}	6.3	4×10^{-6}	5.4	Flame-photometric
56	Ba*	138	85m	8×10^{-9}	8.1	1×10^{-5}	5.0	Flame-photometric
74	W	186	24h	2.5×10^{-9}	8.6	2×10^{-7}	6.7	Thiocyanate-reducing agent
75	Re	187	17h	3×10^{-10}	9.5	1×10^{-6}	6.0	Thiocyanate
79	Au*	197	2.7d	6×10^{-10}	9.2	2×10^{-7}	6.7	Rhodanine
80	Hg	196	65h	†2×10^{-8}	7.7	3×10^{-5}	4.5	Dithizone
81	Tl	203	3y	7×10^{-6}	5.2	2×10^{-5}	4.7	Iodine
82	Pb	208	3.3h	2.5×10^{-5}	4.6	2×10^{-6}	5.7	Dithizone
83	Bi	209	5d	5×10^{-6}	5.3	2×10^{-6}	5.7	Dithizone

* Elements for which activation analysis methods have already been used.

† Sensitivity based on γ-counting with scintillation counter.

Half-lives in italics or boldface indicate those for metastable or ground state daughter, respectively.

TABLE 3. *Comparison of sensitivities of radioactivation method with those of conventional methods for the elements unknown in marine samples*

Atomic No.	Element	Sensitivity of radioactivation analysis				Sensitivity of conventional analysis		
		Mass No. of parent	Half-life of daughter	Sensitivity (g)	Sensitivity index	Sensitivity (g)	Sensitivity index	Method
44	Ru	104	4.5h	2.5×10^{-8}	7.6	1×10^{-6}	6.0	Thiourea
45	Rh	103	*4.4m*	2.5×10^{-8}	7.6	2×10^{-6}	5.7	Stannous chloride
46	Pd	108	13.6h	2.5×10^{-9}	8.6	5×10^{-7}	6.3	Nitrosophenylamino
49	In	115	54m	2.5×10^{-11}	10.6	2×10^{-5}	4.7	Dithizone
52	Te	126	9.4h	5×10^{-8}	7.3			
72	Hf	180	46d	3×10^{-7}	6.5			
73	Ta	181	**112d**	1.5×10^{-7}	6.8			
76	Os	192	31.5h	4×10^{-8}	7.4	2×10^{-5}	4.7	Thiourea
77	Ir	193	19h	2×10^{-10}	9.7	2×10^{-5}	4.7	Chloroiridate
78	Pt	198	31m	2×10^{-8}	7.7	2×10^{-5}	4.7	Stannous chloride

Half-lives in italics or boldface indicate those for metastable or ground state daughter, respectively.

SENSITIVITY OF RADIOACTIVATION ANALYSIS FOR TRACE ELEMENTS

The term sensitivity is defined as the weight of an element that would produce a measureable amount of radioactivity after it had been irradiated by a given flux of neutrons for a given period of time.

As previously described (Meinke 1955) the general equation governing analysis by activation is

$$\text{Grams of X} = \frac{\text{Act.} \times \text{at. wt.}}{6.02 \times 10^{23} f(\sigma_{at})\ 1 - e^{\frac{-0.693t}{t_{1/2}}}}$$

where Act. is the radioactivity (dis. sec.$^{-1}$), at. wt. is the atomic weight of the isotope activated, f is the flux of neutrons (neutrons cm^{-2} sec.$^{-1}$), σ_{at} is the atomic cross section, t is the period of irradiation, and $t_{1/2}$ is the half-life of the resultant radioisotope. Since at. wt., σ_{at} and $t_{1/2}$ are constants for a given isotope, we see that the weight detected is proportional to the activity, the flux, and the time of irradiation.

Consequently, if we choose a proper neutron flux and irradiation time and evaluate the activity so as to be the lower detection limit of a radioactivity measurement by suitable instruments, we determine the sensitivity of radioactivation analysis under ideal conditions. The sensitivity of the analysis can be improved by increasing the neutron flux, the irradiation time (for long-lived isotopes), and/or the sensitivity of the instruments used for the radioactivity measurements.

Leddicotte and Reynolds (1953) computed the sensitivity of activation analysis for each element assuming a neutron flux of 5×10^{11} neutrons cm^{-2} sec.$^{-1}$ and an irradiation period of ten half-lives or 30 days, whichever was shorter. Jenkins and Smales (1956) assumed a similar irradiation period in their computations, but they assumed a neutron flux of 10^{12} neutrons cm^{-2} sec.$^{-1}$, introduced a time of two hours for the required radiochemical separation, and also considered the detector counting efficiencies for the β- or γ-emitting radioisotopes. Their irradiation period of 1 month, however, seems to be too long for a general analytical procedure.

Recently Schindewolf (1958) computed sensitivities based on a neutron flux of 10^{12} neutrons cm^{-2} sec.$^{-1}$ and irradiation times of 6 minutes and 600 minutes (10 hours). He considered the counting efficiency (using a Geiger counter in most cases) but not the time required for radiochemical separations. We have modified Schindewolf's values in order to make a comparison of the sensitivity of radioactivation analysis with that of conventional methods. His 10-hour irradiation values were changed to include a 30-minute decay period (for chemical separation) after the end of neutron irradiation, and then were multiplied by a gross normalizing factor of 2 to cover chemical yield. While 30 minutes may not be sufficient for

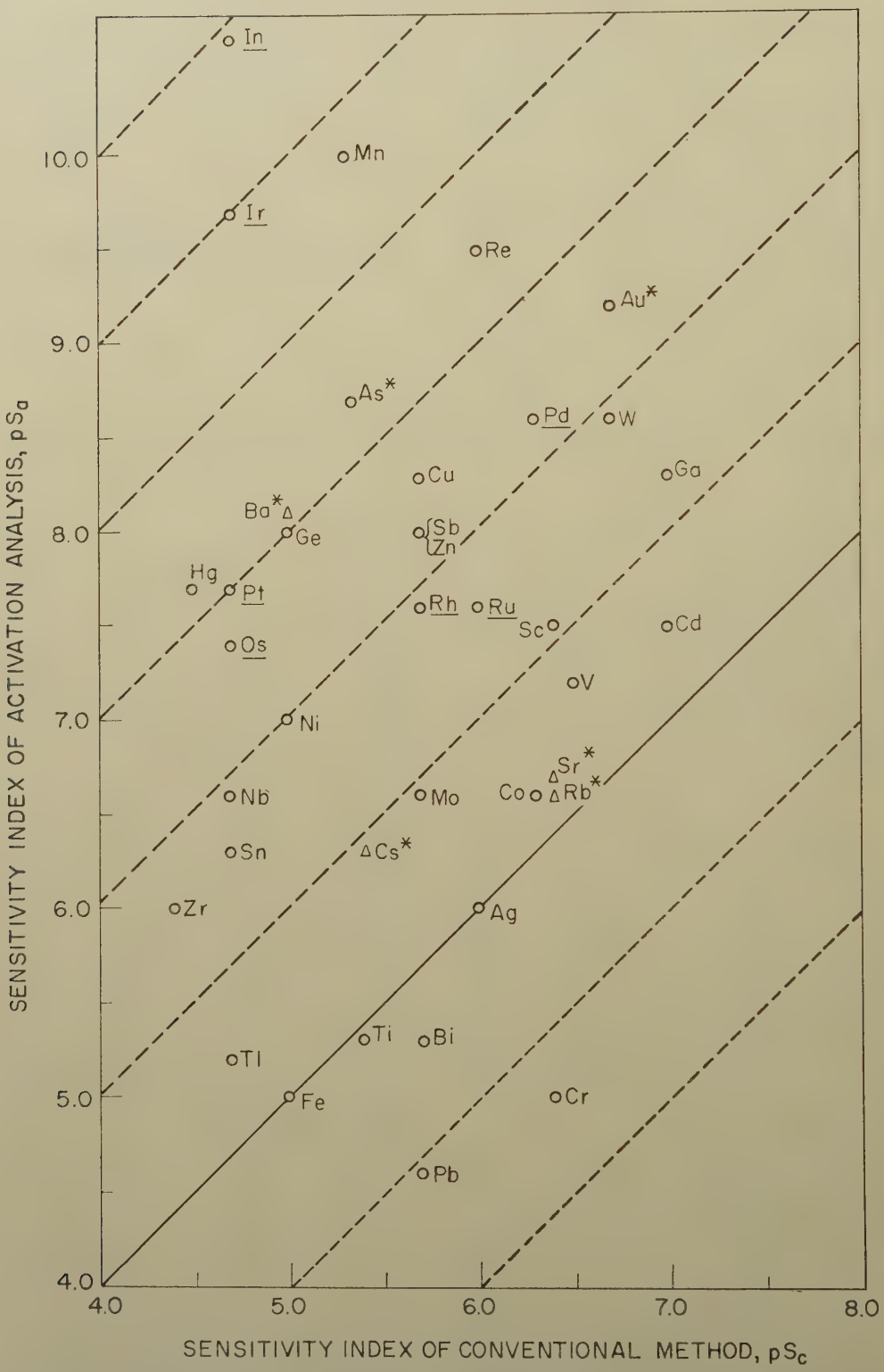

FIG. 1. Comparison of sensitivity of activation analysis with that of conventional methods. ○ spectrophotometric; △ flame photometric; * activation analysis has already been used.

the radiochemical separation in some cases, it is reasonable time when new techniques for separation are taken into consideration. In addition, the measurement of radioactivity of some short-lived isotopes might be carried out by γ-spectrometry with little or no chemical separation. On the whole, the error of the sensitivities may be estimated to be about $\pm 50\,\%$ or less.

For conventional methods, sensitivities quoted are mainly those of spectrophotometry (Sandell 1950), although the values of flame photometry (Meinke 1955) are given for alkali metals and alkaline earths. Although various advantages may be offered by other methods, they were not included here. These sensitivity values for conventional methods were also multiplied by a factor of 2 to make them more comparable to the activation values. The maximum error of determination is estimated to be $\pm 50\,\%$ or less at this level of concentration. The final volume of the solution for measurement was considered to be at least 5 ml for spectrophotometry and 2 ml for flame photometry.

In Tables 2 and 3 the sensitivities of both the activation and the conventional methods are compared. Table 2 includes all the elements of Table 1, except for the lanthanide elements and the strongly radioactive elements. Elements, other than rare gases, which had been reported neither in marine organisms nor in sea water are listed in Table 3. In these tables the unit of sensitivity is not a concentration, but an absolute weight in grams of the element in question. A "sensitivity index" was added in order to facilitate comparison of sensitivities and was defined as the negative logarithm of the sensitivity:

$$pS(\text{Sensitivity index}) = -\log S,$$

where S designates the sensitivity in grams.

In Figure 1 the sensitivity indices for activation analysis, pS_a, were plotted versus those for the conventional methods, pS_c. The solid straight line in the figure indicates the line of equal sensitivity of both methods. Therefore, the domain above the line indicates a superiority of activation analysis over the conventional methods, and *vice versa*. Broken lines in the figure show 10-fold, 100-fold, etc., differences.

In some cases the sensitivity of the conventional methods might be increased by as much as a factor of 10 by using special techniques. In addition the sensitivity of the activation methods might be too high for elements giving short-lived activation products, since a detailed consideration of the radiochemical purification has not been made. Yet, the advantage offered by the application of activation methods to the analysis of a number of elements is evident. The possibility for discovery of elements of the ruthenium- or platinum-groups as well as indium in marine samples appears to be good.

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Midwater Trawling Studies in the North Pacific[1]

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ABSTRACT

A modified version of the Isaacs-Kidd midwater trawl was used for 149 exploratory hauls in the Northeastern Pacific at depths ranging from 20 to 250 meters. Catches are discussed in terms of such factors as diurnal migration, seasonal variation, patchiness, and geographic variation.

There was wide difference between day and night hauls. Geographic variation was marked. Abundance of plankton and fish decreased with increasing distance from the Washington coast, but increased again just south of the Alaskan peninsula. Northward and seaward there was a decrease in number of fish species. There appeared to be definite correlation between catches and an oceanographic boundary at approximately 50° North.

A number of rare fish, one new species, and two leptocephalus larvae were taken.

Consistency of results and close relationship of oceanographic and biological data suggest the usefulness of the midwater trawl as a valuable tool for future investigations of plankton ecology.

INTRODUCTION

This report summarizes the results of midwater trawling studies conducted in the North Pacific by the M. V. BROWN BEAR of the University of Washington, Department of Oceanography, during the summer of 1957. The trawl studies were made on a cruise devoted primarily to research for the International Geophysical Year program.

The author is indebted to many people who have contributed to the development of this report. Dr. R. H. Fleming of the University of Washington provided the primary stimulus for the research and gave considerable assistance in the preparation of the manuscript. Dr. George H. Allen, Humboldt State College, was responsible for trawling operations during the first part of the cruise. Dr. Robert G. Paquette, Chief Scientist of the expedition, made oceanographic data readily available and, with his staff and the ship's crew, made it possible to conduct the field operations with a minimum of effort. Dr. Author Welander of the University of Washington gave unsparingly of his time, and his help with the identification of fishes was invaluable. Particular appreciation is expressed for the meticulous work and unstinting efforts of Mr. Peter McCrery throughout the program.

The trawling studies were primarily exploratory: to find out what animals inhabit the depths under study and also to obtain some idea of their relative abundance. Within these two major objectives, information was desired regarding the horizontal and vertical distribution of trawl-caught animals and the relationship between these distributions and the oceanographic data which were obtained during the course of the work. Figure 1 shows the area covered during the period 22 July to 22 September 1957 and the location of each haul.

METHODS

A modified version of the Isaacs-Kidd midwater trawl (Fig. 2) was used for sampling (Isaacs and Kidd 1953). The cod end was a 0.5-meter plankton net having a mesh opening of ⅛-inch (Dupont Nylon, pattern 281, Marion Textiles Inc., New York, N. Y.), and fitted with a collecting bucket attached by means of a bayonet-type mount.

A total of 149 hauls was made at depths ranging from 20 meters to about 250 meters. For most hauls the net was fished 30 minutes at depth. The total time for each haul was

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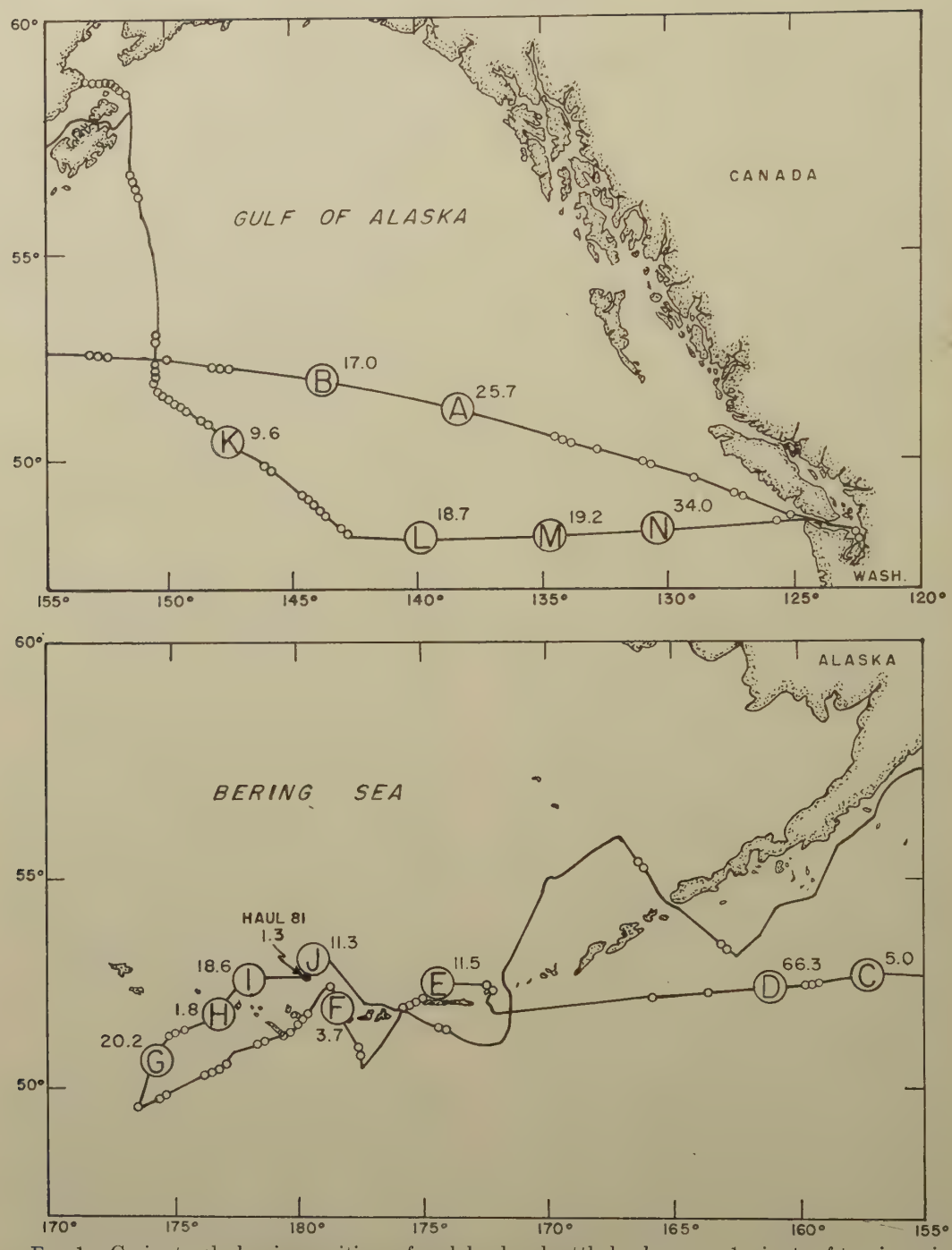

FIG. 1. Cruise track showing positions of each haul and settled volume per 1 minute of tow in major geographical areas.

measured from the time the net first entered the water until the time the haul was terminated and the net removed from the water. All hauls were made with the ship proceeding at one engine full, a speed of about 6.0 knots. The net was released with the ship underway at towing speed and was recovered with the ship's speed reduced to about 4.5 knots.

The catches consisted mainly of the larger zooplankters (euphausiids and pelagic shrimp) and small fish, primarily myctophids. In a number of hauls large catches of crab larvae, copepods, and arrow worms were recorded; however, because of the $\frac{1}{8}$-inch nylon netting in the cod end, animals smaller than 2 mm were never taken in large quantities.

The catches were preserved in 10 per cent formalin and stored in 16-ounce screw-cap jars. In the laboratory adult fish and other large forms were removed from the samples. The settled volume of each catch was then determined by placing the sample in a 500-ml tapered graduate and allowing it to settle for at least 30 minutes. For the purpose of comparison these volumes in milliliters were then divided by the total time of the haul in minutes. The resulting numbers are recorded as the corrected plankton volumes and represent the volume of material caught per minute. After the completion of each volume determination the catch was examined and the dominant planktonic animals were noted. All fish larvae were removed, and the fish and larvae were then examined. Nearly all of the adult fish were identified to species; the larvae were usually identified to family. The maximum and minimum total lengths for each species of fish were recorded for each haul. Aron (1958) has presented the raw data for each haul, including corrected plankton volume; dominant planktonic animal; number and size of each species of adult fish; number and size of larval fish, usually according to family or genus; and depth, time, date, and position of haul.

Of the 149 midwater trawl samples only 143 were analyzed. Four of the samples were lost during a storm when the lashings which secured the sample cases to the deck were broken and the cases were washed overboard. One sample was discarded at sea because of extensive fouling caused by jellyfish, while another sample was used for isotope studies. Although this paper considers the results from all of the hauls made during the cruise, it considers in detail only the hauls shown in the fourteen major areas indicated by letters A through N in Figure 1.

GEOGRAPHIC VARIATION

In order to evaluate the geographic variation in plankton abundance, consideration must be given to four sampling variables: (1) diurnal migration, (2) vertical stratification, (3) seasonal variation, and (4) local plankton "patchiness." Observed variations in plankton volumes between areas may not be a reflection of actual differences between areas, but may be due to any one, or any combination, of these four sampling variables.

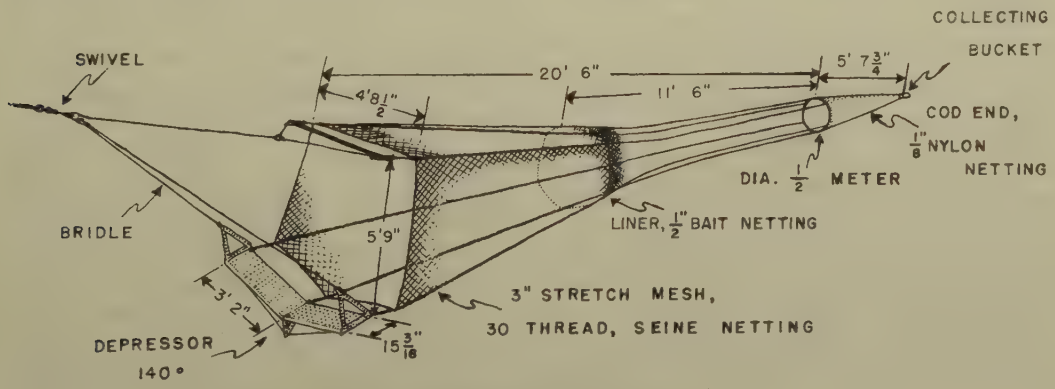

FIG. 2. Modified Isaacs-Kidd trawl.

In an attempt to eliminate fluctuations resulting from diurnal migrations, hauls made from one hour after darkness until daybreak were treated separately from hauls made during daylight hours. Variations resulting from vertical stratification were treated by grouping hauls according to depth. In Table 1 the data are grouped by time and depth, and averages are given for plankton volume and numbers of fish, numbers of fish larvae, and numbers of species of adult fish. In the compilation of this table eight hauls were not used, primarily because of trouble with the gear during the course of these hauls.

The data in Table 1 indicated wide differences between day and night hauls, with the differences diminishing in the deeper hauls. For night hauls there is a general decrease in plankton volume with an increase in depth, and for day hauls the reverse holds true. In the night hauls the numbers of fish and of fish larvae, and the average number of species of adult fish all decrease with depth, except for an increase in the deepest hauls.

Because of the nature of the cruise, no satisfactory measure of seasonal variations was obtained; however, at one point the cruise track crossed after an interval of 45 days. At the point of crossing two hauls are available that were taken during the same time of the day and at the same depth. The haul taken at the beginning of the cruise (July 29) had a corrected volume of 2.1, while the haul taken 45 days later (September 9) had a corrected volume of 2.2. The dominant animal on both occasions was a calanoid copepod.

TABLE 1. *Trawl catches during day and night hauls*

Depth range (m)	Time	Number of hauls	Average plankton vol. ml/min.	Average number per haul		
				Fish	Fish larvae	Species of adult fish
20–30	Day	4	1.0	1.0	5.8	0.5
	Night	25	29.2	67.5	30.5	3.0
31–60	Day	11	1.6	2.5	3.7	0.5
	Night	31	14.0	28.0	10.2	3.2
61–120	Day	6	2.0	2.2	1.2	1.2
	Night	9	16.4	10.3	2.6	2.4
121–250	Day	19	5.8	9.1	2.3	1.0
	Night	30	7.0	17.3	7.2	4.3

Seasonal variation can also be examined by considering the first and last legs of the cruise. These legs were separated by a period of about 50 days; however they were spatially relatively close together. The average corrected volumes for the night hauls made at depths of 30, 60, and 225 meters in areas A and B (July 26–27 and July 27–28) were 25.7 and 17.0. The average corrected volumes for the night hauls at the same depth for areas L and M (September 19 and 20) were 18.8 and 19.2.

Pelagic shrimp and euphausiids dominated these hauls, the shrimp being more abundant during the last leg, the euphausiids during the first leg. These distributions are complicated by the existence of a rather sharp oceanographic boundary at about 50° N Latitude which separates the northern leg of the cruise from the southern portion. Figure 3 shows that in the south (Area L) a layer of relatively warm water (57–60°F) was found in the upper 40 meters. In the north (Area B) the water in this layer was colder (46–54°F). This oceanographic condition, which marks the northern border of North Pacific Drift water, appears to have concentrated the major plankton abundance in the southern hauls at a slightly lower depth than in the northern hauls.

It appears that seasonal variation plays a relatively unimportant role in the analysis of the trawling data from this cruise. A satisfactory statement about the role of seasonal variation would require considerably more data than are available.

The fourth variable, which the nature of the gear minimizes by the large sample size, is plankton patchiness—that is, populations in a small area distributed in clouds of various densities (much like fish schools) rather than uniformly. In four successive hauls taken at the same depth, for example, corrected plankton volumes of 6.8, 4.1, 4.4, and 4.9 were obtained. The close grouping of these volumes in comparison to the much larger variations due to diurnal migration, stratification, and geography reduces the importance of plankton patchiness in the study of the trawl results.

The analysis of geographic variation is based primarily upon the night hauls. In

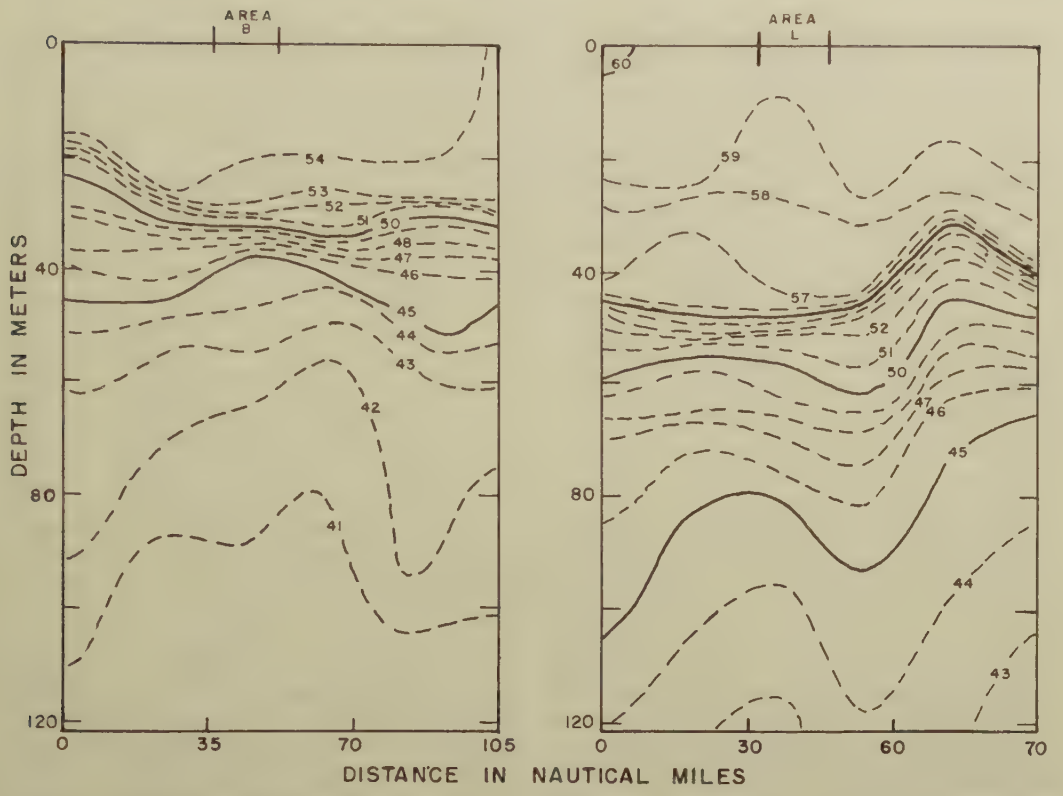

FIG. 3. Bathythermogram sections from areas north and south of 50° N. latitude (temperature in °F.)

fourteen areas shown in Figure 1, a series of three night hauls made at depths of 30, 60, and 225 meters are available for comparison. The corrected volumes for the three depths were averaged to give the relative plankton abundance for each of the fourteen areas. Figures 1A and 1B show the general decrease in plankton abundance as the distance from the Washington coast increases. This decrease continues until a sudden increase in abundance is found in area D, south of the Alaska Peninsula. The average corrected volume for area D (66.3) is more than an order of magnitude greater than the corrected volume of 5.0 in the neighboring area C. Hauls made in the Aleutian Islands region show great variations in relative volumes. Area H, for example, has an average corrected volume of 1.8. It was located between areas G and I, which had average corrected volumes of 20.2 and 18.6, respectively.

The wide variations in relative plankton abundance between areas that are geographically close prompted examination of the oceanographic data taken during the study. A nearly complete bathythermogram record for the cruise course provided the first indication of a possible cause of the great variations in the Aleutians. Some of these data, shown in Figure 4, clearly show that the high catches, dominated by euphausiids, were made in areas of relatively warm, stable water, (area I) while the low catches, dominated by copepods and arrow worms, were made in areas of cold, unstable water (area H). Areas that are intermediate in bathythermic characteristics are also intermediate with respect to their biota. Area J has a corrected plankton volume of 11.3, which is between those of the high and low values for the Aleutian area. In haul No. 81 (area J; see Fig. 1) with a corrected plankton volume 1.3, copepods and euphausiids have about equal quantitative importance.

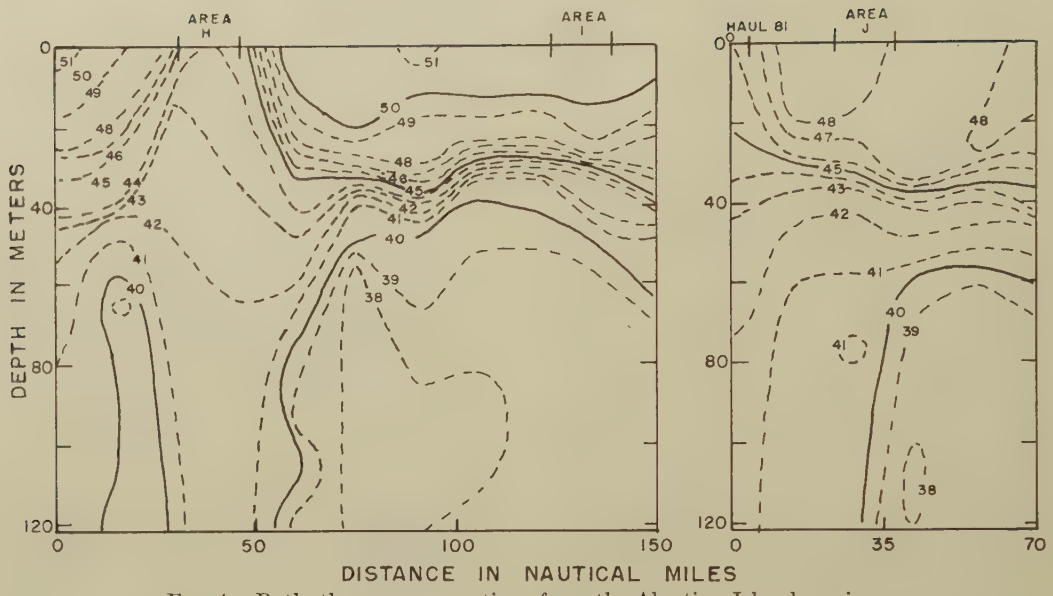

FIG. 4. Bathythermogram sections from the Aleutian Islands region.

The oceanographic variations and the limited number of samples made it difficult to evaluate the relative abundance of plankton in the Aleutian regions. However, the data do indicate that the cold, less stable water is being pushed up from the south, and that the regions north of the islands have a higher standing crop of plankton than have the regions to the south.

An explanation of the high volumes obtained south of the Alaska Peninsula must await further interpretation of the oceanographic results. Previous studies in the area, particularly the NORPAC cruise in 1955 (Fleming 1956), indicate that this is an area of high plankton abundance and is rich in phosphates and other nutrients.

EXPLORATORY RESULTS

Only limited work has been done with the invertebrate portion of the catches. The amphipod, *Parathemisto libellula* was found only in the Bristol Bay-Bering Sea area and in some hauls made near Kodiak. Catches of large shrimp, *Pandalus borealis*, near Kodiak pointed to the possibility of commercially exploitable populations in this area.

Variations in fish fauna were both geographical and vertical. In hauls made near shore, *Sebastodes* spp. and the larvae of three species of flatfish, *Hippoglossoides elassodon*, *Microstomus pacificus*, and *Glyptocephalus rex*, were found. In the northerly inshore waters large numbers of capelin larvae, *Mallotus catervarius*, were taken. *Sebastodes* larvae down to 6 mm in length and *Microstomus* larvae down to 16 mm in length were taken more than 300 miles from the nearest land mass. In the oceanic regions the larvae of the inshore fishes disappeared and myctophid larvae were common.

The fish of the open ocean appear to have widespread geographic ranges. The myctophid, *Lampanyctus leucopsarus*, was ubiquitous, occurring in nearly every haul in the deep ocean. Three other members of the genus, *L. townsendii*, *L. ritteri* and *L. regalis*, were also taken but were less common. *L. townsendii*, was taken only in the most southerly part of the cruise; *L. ritteri* was taken primarily in the more southerly hauls, and *L. regalis* was found west of the Aleutians. With the exception of *Myctophum californiense*, all of the other lantern fishes (*Tarletonbeania crenularis*, *Electrona arctica*, and *Diaphus theta*) taken during the cruise had distributions similar to the distribution of *L. leucopsarus*. *M. californiense* was found only during the southern portion of the cruise.

The stomiatid, *Tactostoma macropus*, and several species of argentinid were found throughout the survey area, although these fish were never as abundant as the myctophids. Less abundant but about equally widespread was the chauliodontid, *Chauliodus macouni*. The melamphid, *Melamphaes lugubris*, was widespread, but seemed more northerly in its distribution than either *T. macropus* or *C. macouni*.

The general pattern of fish distribution in the area surveyed indicates that there is a decrease in the number of fish species as the distance from the coast of Washington increases. This was particularly apparent during the last part of the cruise: the number of species per haul increased as the hauls were taken closer to the Washington coast. This seems related to the occurrence of the North Pacific Drift water, which increases in temperature closer to the coast.

There was a decrease in the number of species in the more northerly waters. This would closely agree with Marshall's observations (1954) that no true bathypelagic fishes exist in Arctic waters.

Definite vertical patterns in the distribution of the more common species were apparent. All of the melamphids taken during the cruise were captured in the 225-meter hauls. The stomiatid fishes were taken mostly below 60 meters. Table 2 shows the vertical distribution of the seven species of myctophids taken during the cruise. Thirteen of the fourteen areas used in plotting the geographic distribution of plankton abundance were used in compiling this table. Area F was omitted because of the absence of fish.

Table 2 shows that *E. arctica* primarily inhibits greater depths than *D. theta*, which is concentrated in the shallower hauls. Insufficient numbers of *M. californiense* are available to make a strong statement concerning its vertical distribution; however, this species seems to be most abundant close to the surface. The distribution of *T. crenularis* is also uncertain. The data point to a fairly wide vertical range; however, based on the condition of the animals at the time of capture, the author feels that this species is primarily a surface dweller, and its capture in the deeper hauls was probably the result of contamination as the net was pulled to the surface. This conclusion is supported by data from hauls not analyzed in Table 2.

The depth distribution of three species of *Lampanyctus* has ecological significance. *L. leucopsarus* ranges primarily in the surface waters, whereas *L. ritteri* was captured mostly in the deeper hauls. These two species, therefore, seem to inhabit different ecological niches. *L. townsendii*, however, is also found only in the surface hauls and appears to be in direct competition with *L. leucopsarus*. Table 3 gives a breakdown of the vertical distribution of *L. leucopsarus* for three areas on the outward leg of the cruise (areas A, B, and C) and three areas on the returning southern portion of the cruise (areas L, M, and N). Table 3 shows that on the southern portion of the cruise *L. leucopsarus* was caught in greatest numbers in the hauls made at 60 meters, while it was caught on the northern portion primarily in the hauls made at 30 meters. *L. townsendii*, on the other hand, was caught only in hauls made on the southern leg of the cruise and was taken in the shallow hauls. The species,

TABLE 2. *Depth distribution of myctophids*

Species	30 meters		60 meters		225 meters	
	No./haul	% occur.	No./haul	% occur.	No./haul	% occur.
L. leucopsarus	79.5	92.3	27.8	100.0	10.4	92.3
L. ritteri	0	0	0.2	15.4	0.7	30.7
L. townsendii	0.3	15.4	0.1	7.7	0	0
D. theta	5.6	61.5	2.0	53.8	1.4	61.5
T. crenularis	0.4	23.1	0.6	38.5	0.4	38.5
E. arctica	0.1	7.7	0.1	7.7	5.8	69.2
M. californiense	0.2	15.4	0	0	0	0

therefore, do not seem to overlap greatly in their vertical distribution in the same area.

The change in depth distribution of *L. leucopsarus* between the first cruise-leg to the north and the returning cruise-leg to the south is probably a reflection of different oceanographic conditions in the two areas. Figure 4 shows the bathythermogram sections made for areas B and L. Here it can be seen that the water at 60 meters in the south is about the same temperature as the water at 30 meters in the north.

At least one new species and a number of rare fish were taken during the cruise. The new species is in the family Stomiatidae and has been assigned the name *Bathophilus flemingi* (Aron and McCrery, 1958).

Two giant leptocephali were taken, one 210 mm and the other 206 mm long. These are particularly interesting, not only because of their large size but because they were taken in an area lacking apodes other than nemichthyids. At present there are no indications of what the adult form of the larvae may be; however, some significance may be attached to the fact that they were taken in water of the North Pacific Drift.

Among other catches of rare and possibly new species were included ten specimens of *Melamphaes lugubris*; several species in the family Bathylagidae; one species in the family Microstomidae, probably *Nansenia candida*; five specimens in the family Nemichthyidae, probably *Avocettinia gilli*; one specimen of a hatchet fish in the family Sternoptychiidae; a number of specimens in the family Paralepidae, probably all *Lestidium ringens*; and also three specimens of *Aristostomias scintillans*, belonging to the family Melanostomiatidae.

It should be noted that the capture of three specimens of *A. scintillans* brings to five the number of specimens of this fish caught in the Pacific. A single specimen of this fish was caught by the University of Washington Department of Oceanography in 1956 off the Washington coast (unpublished record), and the first recorded specimen was taken in 1915 off the California coast (Gilbert 1915). One specimen, caught during the present work, was in nearly perfect condition when it was removed from the net. The light organ at the tip of the barbel was observed to have a pinkish glow. The subocular luminous organ glowed an intense red, alternating several times between the green flashes of the postocular luminous organ.

TABLE 3. *Depth distribution of* L. leucopsarus *in northern and southern portions of cruise*

Depth (m)	Number of Specimens					
	Northern portion			Southern portion		
	A	B	C	L	M	N
30	73	22	21	7	17	23
60	8	11	7	29	29	109
225	15	9	4	8	7	10

QUANTITATIVE EVALUATION OF MIDWATER TRAWL

There are no satisfactory estimates of the volume of water filtered by the different sections of the net, nor are there any measurements of the catching power of the trawl in relation to other nets. It is therefore difficult to make quantitative comparisons of the trawl catches and catches by other standard plankton-sampling devices.

Maximum values for the filtering capacity of the trawl can be computed by multiplying the cross-sectional area of the mouth opening

TABLE 4. *Quantitative evaluation of the midwater trawl*

	Section of the net		
	Front end (3″ netting)	Middle section (3″ netting, lined with ½ netting)	Cod end (⅛″ netting)
Cross-sectional area of mouth opening in m^2	5	1.3	0.2
Water strained[a] m^3/min/	930	245	36
Plankton concentration[b] g/m^3	0.004	0.016	0.110
Fish[c] g/m^3	0.0008	0.003	0.020

[a] For ship speed of 6 knots.

[b] Assuming average catch of 20 ml/minute (4 g/minute).

[c] Assuming catch of 1 fish per minute (0.75 g/minute).

by the length of the water column through which the net passes. Table 4, based upon a ship's speed of 6 knots, gives the maximum volumes of water strained by different sections of the net during one minute of trawling.

During the night hauls (see Table 1) the average plankton volume in the upper 120 meters was about 20 ml per minute of trawling, and about 1 fish was caught per minute of trawling. Dividing the average plankton catch (based on settled volume) by a factor of 5 (Redfield 1941) yields an approximate value for the weight of the plankton in grams. Applying the factor to the value given above gives 4 grams/minute. The average weight of each fish caught was about 0.75 gram. Using these weights, Table 4 gives the weights of plankton and fish per cubic meter of water, determined by assuming: (1) that all water through which the net passes is filtered, (2) that each section of the net operates independently, and (3) that when an animal passes through the mouth opening of the particular section of the net it is caught. As there is probably high escapement of plankton through the 3-inch mesh of the net, the concentration estimated by using the mouth opening of this section is minimal. Escapement decreases in the section lined with ½-inch bait netting and decreases further in the cod end of the net. As the forward sections of the net may serve to guide the catch into the cod end, the plankton concentration estimated using the mouth opening of this section is probably high. A realistic value probably lies between the concentrations obtained for the middle section of the net (0.016 gram/m^3) and the cod end (0.11 gram/m^3).

The escapement of fish through the 3-inch section of the net is probably considerably less than the escapement of plankton. It is also probable that fish escapement through the section lined with ½-inch bait netting is low. A realistic value for the weight of fish per cubic meter of water, therefore, probably lies between 0.0008 and 0.003 gram.

It must be emphasized that the plankton concentrations primarily refer to plankton populations a step higher on the food chain than those caught in gear such as the Clarke-Bumpus net or the standard 0.5-meter plankton nets. The fish caught by the net are probably one step higher on the food chain than the plankton caught by the net. The difference in weight of fish and weight of plankton is about one order of magnitude, a difference which could be expected between different steps on the food chain.

DISCUSSION

The limited amount of data and the extent of the area under consideration make definite conclusions difficult. The data presented in this report must be used with caution and with the understanding of their many limitations.

It must be remembered that all data referring to abundance are relative values. There are no measurements of how much water is actually filtered by the net, nor is there any indication of the effect of clogging. Although the ship's engines were kept at the same speed for nearly all of the hauls, the relative speed of the net through the water varies according both to weather and to currents at depth and on the surface. These variations in towing speed probably are unimportant, although they must be investigated eventually.

The measurements of seasonal variation are obviously insufficient. It is possible, although not probable, that the geographic variations are in fact seasonal variations.

The following general conclusions are made for the time period involved in the study and concern only those animals caught in the midwater trawl:

(1) The abundance of both plankton and fish and the number of species of fish decreases with increasing distance from the Washington Coast out to the area south of the Alaska Peninsula (area D), where there is a sudden increase in plankton abundance. This increase may be related to the fact that the area is on the border of the Alaska Gyral and the Alaska Coastal Region and is rich in phosphates and other nutrients.

(2) The area around the Aleutian Islands is characterized by large variations in the relative abundance of plankton in relatively small geographic areas. These variations are closely associated with the oceanography

of the areas involved. Areas of stable water conditions have a large standing crop, while areas of unstable water conditions and extensive mixing have a low standing crop. The area to the north of the Aleutians seemed richer than the area directly to the south.

The low standing crop in areas that are oceanographically unstable may be a real index of low productivity. The results shown in this paper for the zooplankton closely agree with results obtained by Gran and Braarud (1935), Riley (1942), and Sverdrup (1953) for their phytoplankton work. These workers all demonstrated that where the surface mixed layer was deep, productivity was low in spite of high nutrient concentrations. If phytoplankton production has a low average rate, the establishment of large populations of grazing animals is obviously impossible.

(3) There appears to be an oceanographic boundary at about 50° N latitude. South of this boundary the waters of the Pacific Drift are encountered and fish species not taken to the north are found. There is a change in the vertical distribution of plankton abundance in this region, with the peak abundance occurring deeper than in waters to the north. The presence of this boundary is also reflected in the vertical distribution of *L. leucopsarus*, the most abundant fish taken during the cruise. North of 50° this fish is most numerous at 30 meters, while south of 50° it is most abundant in the hauls made at 60 meters.

Future studies of the type described must be extended to greater depths. The daylight hauls show the greatest concentration in the deeper hauls (Table 1), and the much higher concentration near the surface at night indicates that the bulk of the material captured must be below 250 m during the daylight hours.

The modified Isaacs-Kidd midwater trawl stands as one of our best tools in the investigation of the macroplankton and the small nekton. The close relationship between the oceanographic data and the biological data and the consistency of the results are strong points in favor of the gear. It may also be important to note that the catch content of the midwater trawl closely resembles the stomach contents of the salmon (Allen and Aron 1957).

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Antibacterial Activity of Antarctic Marine Phytoplankton[1]

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ABSTRACT

Water and phytoplankton samples from the Weddell Sea were assayed for their antibacterial activity during the 1957–58 Argentine Antarctic Expedition. Four of seven sea water samples contained sufficient phytoplankton in volumes of 1 to 500 ml to inhibit bacterial growth. At three hydrographic stations phytoplankton retained by a coarse zooplankton net was inhibitory in concentrations as small as 100 parts per million on a wet volume basis (5 ppm dry weight basis). This antibacterial substance, which inhibited Gram positive organisms to a greater extent than Gram negative organisms, was active in fresh preparations, stable at 60°C for 30 min., labile when heat dried at 85°C for 40 min., water soluble and filterable. Phytoplankton in the stomach of euphausiids, *Euphausia superba*, also exhibited similar antibacterial properties. Such euphausiids, the staple diet of the penguins examined, apparently modify the gastrointestinal microflora of penguins.

INTRODUCTION

A number of investigators have reported that certain Antarctic birds were "bacteriologically sterile" (Ekelöf 1908, Gazert 1912, Pirie 1912, McLean 1919, and Bunt 1955). A recent study of the gastrointestinal microflora of Antarctic birds (Sieburth 1958) conducted aboard the icebreaker GENERAL SAN MARTIN during the 1957–58 Argentine Antarctic Expedition indicated that the antibacterial property of certain dietary materials was at least in part responsible for these reports. Euphausiids (*Euphausia superba*), the sole diet of the penguins studied, exhibited marked antibacterial properties which inhibited the development of aerobic bacteria in some birds and all bacteria in some gastrointestinal segments of other birds. The inhibitory material was located in the phytoplankton laden stomach contents of the euphausiids. Phytoplankton in sea water and plankton net samples obtained during the voyage into the Weddell Sea exhibited a similar antibacterial activity. The antibacterial (Pratt *et al.* 1944) and antialgal (Proctor 1957) properties of freshwater algae have been shown. The presence of antibacterial substances in sea water has been recognized (ZoBell 1936, Ketchum *et al.* 1949, and Orlob 1956). The production of antibiotics by sea water phytoplankton was postulated by Steemann Nielsen (1955) on the basis of respiration studies. The purpose of this paper is to record in the oceanographic literature the demonstration of antibacterial activity of marine phytoplankton and its effect on flora and fauna.

The author expresses his sincere appreciation to Capitán de Fragata Luis R. A. Capurro, the captain of the icebreaker ARA GENERAL SAN MARTIN, for the provision of facilities and his interest in this study and to the officers and men in the oceanographic laboratory for their cooperation.

ASSAY OF ANTIBACTERIAL ACTIVITY

All samples were collected at the hydrographic stations made by the GENERAL SAN MARTIN in the Weddell Sea. The surface water samples were collected in sterile bottles to windward as the ship stopped. The plankton net samples were the jelly (approximately 200 ml) that adhered to the surface of a five-foot eighth-inch mesh zooplankton net towed at speeds less than five knots for five minutes. This was the only net aboard, and although it was unsuitable for collecting all types of phytoplankton, it apparently permitted some of the "jellylike" *Halosphaera* species to adhere to the net while allowing most of the diatoms to pass.

[1] This study was supported by the Arctic Institute of North America (subcontract ONR-191), the Argentine Navy, Virginia Polytechnic Institute, and the U. S. Office of Naval Research.

Algae in the water samples were concentrated on sterile HA Millipore membranes (Millipore Filter Corp., Watertown, Mass.) which were rinsed with filtered autoclaved sea water or physiological saline. The membranes were placed algae side down on a pad soaked with Eugon broth (BBL). The test organisms, which consisted of *Micrococcus ureae*, a diphtheroid-like organism and one typical (rapid lactose-fermenting) and two atypical (delayed lactose-fermenting) strains of *Escherichia coli*, were streaked on the upper sterile surface of the membrane, and growth was compared with that on the broth control. One and five ml aliquots of serial decimal dilutions of the plankton net samples were also concentrated on Millipore membranes and assayed by the same procedure.

A summary of the minimum inhibitory concentrations of phytoplankton in the sea water and net samples is given in Table 1. Of the seven water samples tested, four had a sufficient quantity of inhibitory substance to be detected in the residue from half a liter or less. The results for one sample (H-2) which was very active, are shown in Table 2. The concentrate from 10 ml was the most active, and the Gram positive test organisms were more susceptible than the Gram negative organisms tested. For the three net samples assayed the minimum inhibitory concentrations ranged from a 10^{-4} to a 10^{-6} dilution on a wet volume basis. The results on the highly active sample H-5 are given in Table 3. The Gram positive organisms were much more susceptible than the Gram negative organisms. Three of the four test organisms were markedly inhibited at a dilution of 10^{-6}, which is equivalent to a concentration of 0.0001 per cent (100 parts per million) on a wet volume basis or 5 ppm on a dry weight basis. Dilutions between 5×10^{-3} and 10^{-2} lost their antibacterial activity and became growth enhancing.

TABLE 2. *Antibacterial activity of phytoplankton in sea water sample H-2 when concentrated and tested on membrane filters*

0 = no detectable growth; other values estimated by comparison with broth control.

Sea water filtered ml	Growth of test organisms			
	Gram positive		Gram negative	
	Micrococcus ureae	Diphtheroid-like	*E. coli* (typical)	*E. coli* (atypical)
Broth control	3	1	3	3
1	1	0	2	2
10	0	0	0	0
100	0	0	1	2
500	0	0	0	1

PROPERTIES OF THE ANTIBACTERIAL MATERIAL

The composition of the plankton algae studied varied from station to station. The most active samples appeared to consist mainly of *Halosphaera* species, while those that were mainly diatoms were weak or inactive. The substance was active in fresh samples, maintained its activity on refrigera-

TABLE 1. *The minimum volume of sea water and the maximum dilution of phytoplankton net concentrates which produced antibacterial residues on membrane filters*

Hydrographic station number	Location		Sonic depth in fathoms	Minimum inhibitory concentrations	
	Lat. S.	Long. W.		Sea water filtered ml	Phytoplankton dilution*
1	59° 01.0′	28° 18.0′	1540	100	ND
2	66° 59.6′	20° 47.7′	2400	1	ND
3	71° 44.0′	15° 56.0′	640	>300	ND
4	71° 58.0′	15° 43.0′	170	>400	10^{-5}
5	73° 27.9′	21° 32.7′	120	ND	10^{-6}
6	75° 30.0′	29° 00.0′	143	>300	NP
7	76° 34.0′	30° 50.0′	164	500	NP
9	72° 27.9′	33° 08.0′	2050	100	10^{-4}

* Log dilution of phytoplankton adhering to surface of zooplankton net (average moisture 95%); ND = not determined; NP = no phytoplankton on net.

TABLE 3. *Antibacterial activity of phytoplankton adhering to the surface of a zooplankton net (Sample H-5)*

Aliquots of serial decimal dilutions were concentrated and tested on membrane filters. 0 = no detectable growth; other values estimated by comparison with broth control.

Phytoplankton Log. diln.	Growth of test organisms			
	Gram positive		Gram negative	
	Micrococcus ureae	Diphtheroid-like	*E. coli* (typical)	*E. coli* (atypical)
Broth control	2	1	3	3
10^{-2}	3	2	5	5
5×10^{-3}	3	0	4	4
10^{-3}	0	0	3	2
5×10^{-4}	1	0	3	1.5
10^{-4}	0	0	2	2
5×10^{-5}	0	0	2	1
10^{-5}	0	0	1	0
5×10^{-6}	0	0	3	1.5
10^{-6}	0	0	3	1
5×10^{-7}	1	1	3	3
10^{-7}	1	1	3	3

tion, (5°C for 10 days), was water soluble, and filterable. The effect of trituration and heat on the antibacterial activity of sample H-5 is shown in Table 4. Disruption of the cells by grinding with glass powder followed by rinsing apparently reduced the activity of the material. Holding 1 per cent suspensions at 60°C showed a marked reduction in activity after 5 minutes, no effect after 15 and a slight increase after 30 minutes. This heat treatment may have initially destroyed some of the material on the surface and later weakened the cells to permit a greater liberation of the antibacterial substance. Dry heat at 85°C for 40 minutes reduced the minimum inhibitory concentration of H-5 to 0.5 per cent on a dry weight basis. The moisture content of the net samples ranged between 94 and 96 per cent, and the pH range was from 4.62 to 6.17. Antibacterial activity is not ascribed to the acid reaction, since the pH of the most active dilutions (10^{-3} to 10^{-6} in buffered broth) was pH 7.1.

EFFECT ON BACTERIAL ECOLOGY

During the assay of the sea water samples the algae-free Millipore filtrates became turbid and much bacterial sediment formed

TABLE 4. *Effect of heat and trituration on the antibacterial activity of phytoplankton (Sample H-5)*

Aliquots of log dilutions were concentrated and tested on membrane filters. 0 = no detectable growth; other values estimated by comparison with broth control.

Treatment and concentration Log. diln.	Growth of test organisms			
	Gram positive		Gram negative	
	Micrococcus ureae	Diphtheroid-like	*E. coli* (typical)	*E. coli* (atypical)
Broth control	2	1	3	3
No treatment				
10^{-2}	0	0	0	1.5
10^{-4}	0	0	3	3
10^{-6}	2	1	3	3
60°C—5 min.				
10^{-2}	2	1	1	1.5
10^{-4}	2	1	3	3
10^{-6}	2	1	3	3
60°C—15 min.				
10^{-2}	0	0	0	0
10^{-4}	0	0	3	3
10^{-6}	2	1	3	3
60°C—30 min.				
10^{-2}	0	0	0	0.5
10^{-4}	0	0	3	3
10^{-6}	0	0	3	3
Trituration (glass powder)				
10^{-2}	0	0	0	0
10^{-4}	2	1	3	3
10^{-6}	2	1	3	3

on standing, while the original samples containing algae remained clear. In addition to its effect on the development of bacteria in sea water rich in active algae, the antibacterial properties of plankton algae also appear to modify the bacterial flora of organisms feeding either directly or indirectly on phytoplankton.

Euphausiids (*Euphausia superba*) feed on phytoplankton. Three of six immature forms obtained in plankton samples inhibited the Gram positive test organisms. A number of adult forms obtained at Half Moon Island in the South Shetland Islands were dissected, stored at 0°C for a week, after which Eugon broth dilutions were assayed for their antibacterial activity (Table 5).

TABLE 5. *Effect of euphausiid (Euphausia superba) segments on bacterial growth*

Euphausid segment Log. diln.	Growth of test organisms*			
	Gram positive		Gram nagative	
	Micrococcus ureae	Diphtheroid-like	*E. coli* (typical)	*E. coli* (atypical)
Broth control	2	1	3	3
Eye				
10^{-1}	2	1	5	4.5
10^{-2}	2	1	3	3
10^{-3}	2	1	3	3
Stomach contents				
10^{-1}	0	0	5	4
10^{-2}	0	0	4	3.5
10^{-3}	0	0	3	3
Muscle tissue				
10^{-1}	2	1	5	4
10^{-2}	2	1	3	3
10^{-3}	2	1	3	3

* Luxuriance of growth of the test bacteria on broth dilutions of euphausiid segments. 0 = no detectable growth; other values estimated by comparison with broth controls.

TABLE 6. *Correlation between the bacterial population and the antibacterial activity of gastrointestinal material from a gentoo penguin (Pygoscelis papua) feeding on euphausiids (Euphausia superba)*

Gastrointestinal segment	Number of organisms per gram		Growth of test coliforms*			
	Total aerobes	Total anaerobes	3-1	4-1	4-2	8-1
Broth control	—	—	2	3	3	2
Proventriculus	$<10^2$	<10	0	1	0	0
Central intestine	4.9×10^5	3.1×10^5	2	5	5	5
Terminal intestine	2.4×10^7	3.7×10^7	2	4	4	0

* Ability of organisms to grow on 10 per cent broth suspensions of gastrointestinal material. 0 = no detectable growth; other values estimated by comparison with broth control.

The Gram positive organisms were inhibited only by the phytoplankton laden stomach contents. All three segments enhanced the growth of the three *E. coli* strains.

A number of penguins feeding on euphausiids were free of a microflora (capable of being grown on standard media for intestinal bacteria) in their proventriculus or ventriculus contents, while bacterial forms were present in Gram stained smears from these materials. The bacterial population and antibacterial activity of gastrointestinal material from a gentoo penguin feeding on euphausiids is shown in Table 6. The proventriculus contents were free of a cultivable flora and possessed a marked activity against four strains of *E. coli*. Material from the central intestine was growth enhancing rather than inhibitory, and organisms belonging to the Providence group of *Enterobacteriaceae* were present in good number. Material from the terminal intestine was not as growth enhancing as that from the central intestine, which may have been due to the accumulation of by products from the relatively large bacterial population.

DISCUSSION

Approximately half the water and plankton samples assayed contained phytoplankton that had a detectable antibacterial activity. A higher occurrence and concentration of antibacterial algae may be present in the richer phytoplankton area in the Antarctic Arc (Harvey 1955) than in the area studied. In some water samples the algae concentrate from a small volume was growth enhancing, while that from a larger volume was growth inhibiting. Conversely, small concentrations of the algae jelly were inhibitory, while larger concentrations were growth enhancing. Apparently the concentration at which plankton algae is inhibitory for bacterial growth is somewhat critical and varies with the sample. Pratt (1948) observed that the antibiotic yield from *Chlorella* species was higher in dilute than in more concentrated cultures. Apparently the effect of the inhibitory substance is masked by other materials at certain concentrations. However, the concentrations at which antibacterial algae types were present appeared to be sufficient to prevent the development of large bacterial populations in surface water and to retard or modify the gastrointestinal flora of penguins feeding indirectly on plankton algae.

Growth-promoting and growth-inhibiting substances of marine origin have been observed by a number of workers (Negrelli 1958). The presence of antibacterial sub-

stances in sea water has been recognized, but the specific source of such substances has only been suggested. In discussing the natural brake upon the development of planktonic bacteria in the open sea, Harvey (1955) states "it is an outstanding question why offshore sea water, which contains sufficient nutriment for the production of several million bacteria per cubic centimetre . . . normally supports a population of no more than 10–200 bacteria per CM.[3] as free living planktonic cells." A heat-labile bactericidal factor in sea water which affected sewage organisms was reported by ZoBell (1936). Ketchum *et al.* (1949) and Vaccaro *et al.* (1950) studied the viability and dispersal of coliform organisms in sea water and observed a bactericidal substance that was heat-labile, chlorine sensitive, increased on aging, and underwent a seasonal variation. Orlob (1956) found that bactericidal agents such as sunlight, bacteriophage, and salinity were of negligible importance in the viability of sewage bacteria in sea water. A bactericidal agent was observed by Orlob which was biological in nature, heat and chlorine sensitive, and filterable, and which affected pathogenic organisms to a greater degree than non-pathogenic organisms. Chlorellin, an antibacterial substance produced by the freshwater species of *Chlorella*, was described by Pratt *et al.* (1944). Spoehr *et al.* (1949) found that this substance which was not detected in fresh cells resulted from the photooxidation of unsaturated fatty acids. Steemann Nielsen (1955) found that oxygen consumption in dilute cultures of *Chlorella* and a marine diatom was less in light than in dark bottles and presumed that this was due to the production of antibiotics by the algae.

Data presented in this paper indicate that certain species of phytoplankton liberate a water soluble filterable substance or substances which exerts a differential antibacterial activity. This material is capable of retarding bacterial development in surface sea water and in the gastrointestinal contents of penguins that have fed on phytoplankton-eating crustaceans. It is possible that these antibacterial substances are not restricted to the rich phytoplankton waters of the Antarctic but are of general occurrence and vary with the type and abundance of plankton algae. Since most marine animals obtain their food either directly or indirectly from marine phytoplankton, this antibacterial material may have a profound effect on the types and population of bacteria in sea water and marine animals.

ADDENDUM

Since this paper was submitted further observations were made off the West Coast of Palmer Peninsula in the Bransfield and Gerlache Straits during the 1958–1959 Argentine Antarctic Expedition. The data presented in this paper have essentially been verified with the exception that the *Halospharea* like yellow-green mucilaginous colonial algae were quite pleomorphic and appear to be a species of *Phaeocystis*.

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The Phytoplankton of Narragansett Bay[1]

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ABSTRACT

The phytoplankton of Narragansett Bay is described on the basis of 927 unpreserved samples taken at a series of stations from 1952 to 1956. The annual cycle is divided into four natural periods: 1 (winter and spring) with diatoms dominant; 2 (usually late spring, early summer), flagellates dominant; 3 (usually late summer), diatoms dominant; 4 (fall), flagellates dominant. The major features of this cycle, with maxima in the first and third seasons, are largely due to changes in the concentrations of diatoms, principally *Skeletonema costatum*. Although the concentrations of diatoms and of flagellates in any given season are predictable only within wide limits, their average abundance for the entire annual cycle is relatively constant. Average standing crops in the East and West Passages are approximately the same, but the Upper Bay is more than three times as rich as the lower in both diatoms and flagellates. The highly estuarine upper West Passage is characterized by certain neritic dinoflagellates, while the lower East Passage is marked by oceanic diatoms. Microflagellates and *Skeletonema costatum* are outstanding in frequency of occurrence and as dominants. Each of the four seasons is distinguished by certain dominant species. Correlations of the dominance of the most important species with prevailing temperatures reveal apparent temperature preferences, some species being eurythermal as dominants while other dominants are restricted to narrow temperature ranges. From the first to the third or fourth period there is a progressive increase in the number of species represented, the rate of change in species composition, and the spatial heterogeneity of the population. The average annual standing crop is more than two times as great as that in adjacent coastal waters. This difference is explained by the unusual length of the winter-spring diatom flowering in the Bay (January–May), which results from the combined effects of shallowness, moderate nontidal drift, and turbulence generated by tidal activity. The secondary diatom maximum in the Bay and in the coastal waters of southern New England is typically a summer event and usually precedes the major annual breakdown of stratification in the fall.

The plankton populations of estuaries are generally distinguished from those of open coastal waters by stronger gradients in spatial distribution and more pronounced seasonal and annual fluctuations, owing to the greater effectiveness of meteorological changes in the more restricted environment. To get an adequate picture of these populations therefore requires detailed studies of local differences and seasonal changes, extended over a period long enough to show the magnitude of year-to-year variation. Examples are the investigations of Braarud and others in Norway (*e.g.*, Braarud 1945), Steemann Nielsen (1951) in Denmark, and Margalef and associates in Spain (*e.g.*, Duran *et al.* 1956). Comparable studies along the west coast of the North Atlantic are wanting.

Ferrara (1953) and Smayda (1957) have studied the concentrations, species composition, and production rates of phytoplankton in Narragansett Bay as related to environmental factors. Ferrara's observations were made at one station in the upper Bay, Smayda's at three in the lower Bay, each study covering a period of eight months, from early summer to late winter. These investigations demonstrated the extraordinary richness of the Bay phytoplankton and a seasonal cycle of phosphate concentrations different from that in adjacent coastal waters, but they have left unanswered questions as to the course of events during the spring months, and the degree of local and annual variation in the quantity and species composition of the population.

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NARRAGANSETT BAY

Narragansett Bay, an estuary of 100 square miles, empties into Rhode Island Sound (Fig. 1). Large islands divide the Bay into the West Passage, East Passage, and the so-called Sakonnet River. Forty per cent of the total area is less than 30 feet deep, although the East Passage averages approximately 60 feet in depth. The physical oceanography of this region is discussed in considerable detail by Hicks (1959), and a brief description of its hydrography will suffice for present purposes. There is a net inward movement of relatively high salinity water along the bottom in all three passages and a net seaward movement of fresher water in the surface layers. Average salinity values at the surface range from approximately 31‰ at the mouth to 27‰ in the northernmost areas sampled, and surface temperatures vary seasonally from about −1 to +25°C. Stratification is limited by tidal mixing: in most open waters of the Bay, temperature and salinity differences between surface and bottom waters are less than 3.5° and 1‰ in summer and less than 2.5° and 2.5‰ in winter and spring (Hicks 1953).

SAMPLING PROGRAM AND METHODS

The results here presented are based on several series of weekly phytoplankton col-

FIG. 1. Narragansett Bay, showing station locations.

TABLE 1. *Weekly sampling programs*

Sta.	1952	1953	1954	1955–1956
W1	July 14–Nov. 10	May 13–Oct. 15		
W2				Sept. 22–Oct. 22
W3	July 9–Nov. 10			
W4	July 9–Nov. 10			
W5				Sept. 22–Oct. 22
W6	Nov. 20		Oct. 4	Sept. 22–Oct. 22
W7	July 14–Nov. 10	May 14–Oct. 13	Jan. 6–Nov. 3	
W8				Sept. 22–Oct. 22
W9	July 17–Nov. 12	May 14–Oct. 15	Jan. 6–Nov. 3	Sept. 22–Oct. 22
E1				Sept. 26–Oct. 22
E2				Sept. 26–Oct. 22
E3				Sept. 22–Oct. 22
E4	July 17–Nov. 12	May 14–Oct. 13		
E5	July 17–Nov. 12	May 14–Oct. 13		
E6				Sept. 22–Oct. 22

lections made during the years 1952–1956 at various localities in the Bay, as outlined in Table 1. With the exception of those from Station W6, the 1952 and 1953 samples formed part of another investigation and were taken at the bottom, at depths of 4 to 14 feet. There are, however, in the entire body of data, some 60 pairs of surface and bottom samples at these same stations, and they show fair to excellent agreement in most instances. Therefore it seems unlikely that a serious error will be introduced by considering the 1952 and 1953 samples as representative of the surface populations. This is desirable so that they may be compared directly with the remaining samples, all of which were taken near the surface. The 1955–56 series, comprising 519 samples, is the most extensive and best distributed coverage, providing a synoptic weekly view of the surface populations throughout the East and West Passages for 13 consecutive months. The samples from all series combined total 927.

In the collection of samples, I am grateful for the assistance of Theodore J. Smayda, Clarence R. Monroe, James E. Masterson, Stanley T. Spink, George A. Spink, and especially Charles B. Perkins and Donald A. Campbell. To Mr. Campbell I am also indebted for the salinity determinations.

Subsamples from a one-gallon or a one-quart water sample were examined in fresh condition within 24 hours of collecting, and the original samples, when held overnight, were kept in refrigeration. The 1952 samples were centrifuged. Comparative counts of raw and centrifuged water then showed that centrifugation of the living cells does not effectively concentrate them: the indicated numbers per liter were erroneously low, and the proportions of the species were somewhat altered, the number of small flagellates being consistently underestimated. Thereafter all samples were examined in the natural state (unpreserved, unconcentrated) in a Sedgewick-Rafter counting cell at 100 magnifications. The amount of water examined for any given species depended on the abundance of the cells, and occasional replicate counts indicated that the numbers of all but the scarcer forms were generally representative of the quart or gallon sample. In the 1955–56 series the accuracy of counts of the rarer species was increased and made more uniform by examining, in every sample, the contents of one ml of water, requiring two refillings of the Sedgewick-Rafter cell.

RESULTS

In the yearly cycle diatoms and flagellates[2] alternate in dominating the phytoplankton of the Bay. A diatom flowering is sustained for about the first five months of the year, flagellate numbers reaching

[2] Including the non-flagellated green alga *Scenedesmus* sp. (which appeared in only two samples) and the four ciliates listed in the Appendix. Of the latter, only *Mesodinium* sp. and *Tintinnopsis* sp. were persistent members of the plankton and rarely comprised more than 5% of the population.

their nadir in January or February and then slowly increasing. In late spring a precipitous decline in diatom concentrations, while flagellates are gradually increasing to their moderate annual maximum, results in an early summer flagellate dominance. Subsequently diatoms regain dominance in one or more intense but brief blooms, usually toward the end of the summer, and thereafter fall off to a minimum in late autumn, when flagellates are again dominant, if only by default. During the year, diatom numbers usually fluctuate between 5 and 40,000 cells/ml (5,000 and 40 million cells/L) with observed extremes of zero and more than 80,000 cells/ml, while annual variations in flagellate concentrations are usually confined to the range 50–5,000 cells/ml (extremes, 17 and 13,000). From these figures it is clear that the flagellates are the conservative and less important element, and that the main features of the phytoplankton annual cycle—the seasonal variations in total standing crop and the alternation of diatom and flagellate dominance—must be largely due to changes in the numbers of diatoms.

This brief description shows that the annual phytoplankton cycle is divided into four natural periods or phases:

Season 1 (winter and spring) with diatoms dominant,

TABLE 2. *Inclusive dates and durations (weeks) of seasons at each station*

Where there is some uncertainty as to whether the data cover an entire season, the beginning or closing date and the duration are shown in parentheses.

		Season							
		1		2		3		4	
	Station	Extent	Duration (weeks)	Extent	Duration (weeks)	Extent	Duration (weeks)	Extent	Duration (weeks)
1952	W1					Aug 18–Sept 29	7	Oct 6–(Nov 10)	(6)
	W3					Aug 18–Sept 29	7	Oct 6–(Nov 10)	(6)
	W4					Aug 18–Sept 15	5	Sept 22–(Nov 10)	(8)
	W7					Aug 25–Sept 15	4	Sept 22–(Nov 10)	(8)
	W9					Aug 25–Sept 15	4	Sept 22–(Nov 10)	(8)
	E4					Sept 1–Oct 13	7	Oct 20–(Nov 10)	(4)
	E5					Sept 1–Oct 13	7	Oct 20–(Nov 10)	(4)
1952–53	W1			(May 13)–July 15	(10)	July 22–Sept 30	11		
	W6	Dec 17–Apr 9	17	Apr 15–May 6	4	May 13–Aug 26	16	Sept 2–Dec 16	16
	W7			(May 13)–July 15	(10)	July 22–Aug 26	6		
	W9			(May 13)–May 20	(2)	May 27–Sept 27	19		
	E4			(May 13)–May 20	(2)	May 27–Sept 16	17		
	E5			(May 13)–May 20	(2)	May 27–Sept 16	17		
1953–54	W6	Dec 23–May 6	23	June 2–Aug 11	11	Aug 18–Sept 29	7		
	W7	(Jan 6)–June 9	(23)	June 16–Aug 4	8	Aug 11–Sept 29	8	Oct 6–Nov 18	7
	W9	(Jan 6)–June 9	(23)	June 16–Aug 4	8	Aug 11–Sept 29	8	Oct 6–Nov 18	7
1955	W2							Oct 4–Nov 21	7
	W5							Sept 22–Nov 14	9
	W6							Sept 22–Nov 7	8
	W8							Sept 22–Nov 21	10
	W9							Sept 22–Nov 21	10
	E1							(Sept 26)–Nov 14	(8)
	E2							(Sept 26)–Nov 28	(10)
	E3							Sept 22–Nov 28	11
	E6							Sept 22–Dec 6	12
1955–56	W2	Nov 28–May 28	27	June 5–Sept 17	16	Sept 24–Oct 15	4		
	W5	Nov 21–May 22	27	May 28–Aug 15	12	Aug 20–Oct 15	9		
	W6	Nov 14–May 15	27	May 22–Aug 15	13	Aug 20–Oct 15	9		
	W8	Nov 28–May 15	25	May 22–Aug 15	13	Aug 20–Oct 15	9		
	W9	Nov 28–May 8	24	May 15–Aug 15	14	Aug 20–Oct 15	9		
	E1	Nov 21–May 15	26	May 22–Sept 24	19	Oct 1–Oct 15	3		
	E2	Dec 6–May 22	25	May 28–Aug 15	12	Aug 20–Oct 15	9		
	E3	Dec 6–May 22	25	May 28–Aug 15	12	Aug 20–Oct 15	9		
	E6	Dec 13–Apr 24	20	May 1–Aug 20	17	Aug 27–Oct 15	8		

Season 2 (usually late spring, early summer), flagellates dominant,
Season 3 (usually late summer), diatoms dominant, and
Season 4 (fall), with flagellates dominant.

In view of the overwhelming importance of changes in diatom numbers in the transition from each season to the next, and in the hope of eventually determining the causes of this cyclic progression, it is logical to define these four periods with respect to major changes in diatom concentrations. Thus each season is defined as a period initiated or terminated by the beginning of a steady increase or decrease in diatoms, indicating an important change in environmental factors affecting the welfare of the diatoms, rather than as a period of diatom abundance or scarcity. Seasons 1 and 3 begin when diatoms begin a steady increase, seasons 2 and 4 when diatoms begin a steady decline.

The dates delimiting these seasons and their durations in weeks are shown in Table 2. Where the lack of data leaves some doubt as to the date of beginning or ending of a season, such date and the duration are shown in parentheses.

From year to year the beginning dates of the first, second, and fourth seasons have varied by only six to eight weeks, while for the third period the variation has been 20 weeks. Whereas the durations of the first and fourth seasons have been relatively constant, those of the two middle periods have varied widely. The transition from the second to the third phase is the least clearly marked of the four, and the distinction between seasons 2 and 3 is, in some years, far less pronounced than in others.

Quantitative

Seasonal variation. The quantitative data are summarized in Tables 3–5, which show the mean concentrations of diatoms, of flagellates, and of the total population (cells/ml) at each station for each of the four phases of the annual cycle. Also included are the averages of these figures by season, indicating approximate mean values for the entire Bay for each period in each year. Although scanty coverage of the Bay may throw doubt on some of these averages, it should be pointed out that in the two periods most open to this criticism (seasons 1 and 4 of 1953, Station W6 only), the station sampled was the most central and the most representative single station in the Bay.

TABLE 3. *Diatoms: average concentration by season, cells/ml*

Station		Season			
		1	2	3	4
1952	W1			14,173	274
	W3			6,940	153
	W4			11,173	965
	W7			14,280	1,503
	W9			3,989	218
	E4			2,740	212
	E5			1,370	34
	Means			7,810	480
1952–53	W1		937	3,297	
	W6	6,640	193	7,029	259
	W7		1,047	54,576	
	W9		1,141	2,700	
	E4		736	6,700	
	E5		248	1,811	
	Means	6,640	717	12,685	259
1953–54	W6	7,185	408	28,278	
	W7	5,931	113	20,695	443
	W9	2,975	109	11,458	662
	Means	5,350	210	20,144	553
1955	W2				137
	W5				399
	W6				284
	W8				138
	W9				208
	E1				34
	E2				29
	E3				492
	E6				255
	Means				220
1955–56	W2	17,635	812	8,421	
	W5	13,744	521	460	
	W6	9,031	283	1,115	
	W8	7,220	134	1,507	
	W9	4,263	76	522	
	E1	19,128	2,483	2,669	
	E2	16,040	416	1,610	
	E3	8,268	187	1,496	
	E6	3,306	182	1,414	
	Means	10,959	566	2,135	

The seasonal means derived in Tables 3–5 are averaged in Table 6 (A) to yield grand average concentrations of diatoms, flagellates, and total cells for each of the four periods. Seasonal grand averages for the entire population show distinct maxima in the first and third phases of the annual cycle, due to changes in the abundance of diatoms. This group reaches its annual maximum in intense blooms during the

TABLE 4. *Flagellates: average concentration by season, cells/ml*

Station		Season 1	2	3	4
1952	W1			153	178
	W3			96	89
	W4			349	133
	W7			127	78
	W9			11	13
	E4			26	53
	E5			18	18
	Means			112	80
1952–53	W1		986	2,371	
	W6	114	3,607	773	828
	W7		942	1,318	
	W9		39	497	
	E4		80	246	
	E5		50	472	
	Means	114	951	946	828
1953–54	W6	528	1,688	430	
	W7	756	1,490	634	1,207
	W9	300	1,295	508	426
	Means	528	1,491	524	817
1955	W2				1,802
	W5				1,095
	W6				415
	W8				594
	W9				383
	E1				2,945
	E2				1,255
	E3				574
	E6				319
	Means				1,042
1955–56	W2	1,257	3,339	1,334	
	W5	596	3,729	1,396	
	W6	369	1,542	413	
	W8	278	1,075	558	
	W9	200	896	247	
	E1	707	4,460	1,755	
	E2	433	3,160	904	
	E3	292	1,803	516	
	E6	93	367	285	
	Means	469	2,263	823	

third season, its minimum in the fourth. The flagellates, which are far less variable, are scarcest in the first period and most abundant in the second.

Annual variation. The deviation of each seasonal mean from the grand average for that season has been calculated, and the means of these deviations are given in Table 6 (B) as percentages of the grand average concentration for each season. For example, the grand average concentration of diatoms in the entire Bay for season 1, all years combined, was 7,650 cells/ml; from year to year the mean diatom concentration for season 1 fluctuated about this value (means shown in Table 3), and the mean of these deviations is 29 % of 7,650. For each phase of the annual cycle the year-to-year variation is considerable, mean deviations ranging from 25 % to more than 50 %, and it is greatest for both diatoms and flagellates in the third season.

In view of the magnitude of variation in phytoplankton abundance in each of the four periods from one year to the next, it is important to determine whether these deviations from mean seasonal values accumulate to produce large fluctuations in the average abundance for entire annual cycles, or are cancelled out in the course of four consecu-

TABLE 5. *Total population: average concentration by season, cells/ml*

Station		Season 1	2	3	4
1952	W1			14,326	452
	W3			7,036	242
	W4			11,522	1,098
	W7			14,407	1,580
	W9			4,000	231
	E4			2,766	265
	E5			1,388	52
	Means			7,922	560
1952–53	W1		1,923	5,668	
	W6	6,754	3,800	7,802	1,087
	W7		1,989	55,894	
	W9		1,180	3,197	
	E4		816	6,954	
	E5		298	2,283	
	Means	6,754	1,668	13,631	1,087
1953–54	W6	7,713	2,096	28,708	
	W7	6,687	1,603	21,329	1,650
	W9	3,275	1,404	11,966	1,088
	Means	5,892	1,701	20,668	1,369
1955	W2				1,939
	W5				1,494
	W6				699
	W8				732
	W9				591
	E1				2,979
	E2				1,284
	E3				1,066
	E6				574
	Means				1,262
1955–56	W2	18,892	4,151	9,755	
	W5	14,340	4,250	1,856	
	W6	9,400	1,825	1,528	
	W8	7,498	1,209	2,065	
	W9	4,463	972	769	
	E1	19,835	6,943	4,424	
	E2	16,473	3,576	2,514	
	E3	8,560	1,990	2,012	
	E6	3,399	549	1,699	
	Means	11,428	2,829	2,958	

TABLE 6. *(A) Grand average concentrations (cells/ml) by season, all stations and all years combined, and (B) mean deviations as percentages of grand averages*

		Season			
		1	2	3	4
(A)	Diatoms	7,650	498	10,694	378
	Flagellates	370	1,568	601	692
	Total	8,020	2,066	11,295	1,070
(B)	Diatoms	29	39	53	37
	Flagellates	44	30	47	45
	Total	28	25	52	25

TABLE 7. *Average concentrations for three complete cycles, grand averages of the three cycles combined, and percentage deviations from grand averages*

	Mean for cycle (cells/ml)	% deviation from grand averages
1952–53 Seasons 1–4		
Diatoms	4,470	−15.8
Flagellates	615	−24.2
Total	5,085	−16.9
1953–54 Seasons 1–4		
Diatoms	6,019	+13.4
Flagellates	761	− 6.1
Total	6,780	+10.8
1955 Season 4–1956 Season 3		
Diatoms	5,430	+ 2.3
Flagellates	1,056	+30.2
Total	6,486	+ 6.0
Grand averages		
Diatoms	5,306	
Flagellates	811	
Total	6,117	

tive seasons so that average standing crops per cycle are relatively constant. The observations provide data for three full and discrete cycles: seasons 1–4 for 1953 and 1954, and season 4 of 1955 through season 3 of 1956. (For the first two cycles, there are possible alternatives, but these include the third and/or fourth periods of 1952, when flagellate numbers were underestimated, as noted above.) Average concentrations for the three cycles are shown in Table 7, together with the grand averages of these means and the percentage deviation of each cyclic average from the grand average. Only one of these deviations is as great as the smallest percentage deviation of the seasonal means (Table 6), and the

TABLE 8. *Average concentrations (cells/ml) arranged to show spatial differences, 1955–56*

	Season				Full cycle
	1	2	3	4	
West Passage					
Diatoms	10,716	386	2,728	221	5,461
Flagellates	583	2,260	884	969	1,095
Total	11,299	2,646	3,612	1,189	6,556
East Passage					
Diatoms	11,686	817	1,797	203	5,623
Flagellates	381	2,448	865	1,273	1,136
Total	12,067	3,265	2,662	1,476	6,759
Upper Bay					
Diatoms	16,637	1,058	3,290	150	8,458
Flagellates	748	3,672	1,347	1,774	1,751
Total	17,385	4,730	4,637	1,924	10,209
Lower Bay					
Diatoms	5,764	145	1,235	273	2,626
Flagellates	216	1,035	402	468	480
Total	5,980	1,180	1,637	741	3,106

maximum cyclic variation of the more important constituent of the population, the diatoms, is only 15.8%. Hence it is clear that for each of the four seasons, the mean concentrations of diatoms, of flagellates, and of the total population vary much more from year to year than do the annual means of these same measures. Thus, although the average abundance of phytoplankton in each phase of the annual cycle can be predicted only within wide limits, the average abundance for entire cycles is fairly constant. This means that for both diatoms and flagellates an unusual abundance or scarcity in any one season tends to be compensated by a commensurate scarcity or abundance in a subsequent phase of the annual cycle.

Spatial variation. In addition to the seasonal and annual fluctuations discussed above, there are spatial differences in the quantity of the phytoplankton, which decreases fairly consistently from the upper parts of the Bay seaward. This is best illustrated in the samples of 1955–56, the only series in which all major areas of both East and West Passages were represented (Tables 3–5). In Table 8, seasonal averages for this cycle are combined so as to yield comparisons of population densities between the upper Bay and the lower Bay and between the West and East Passages. (Because of its central position, Station W6 is not representative of either the upper or the

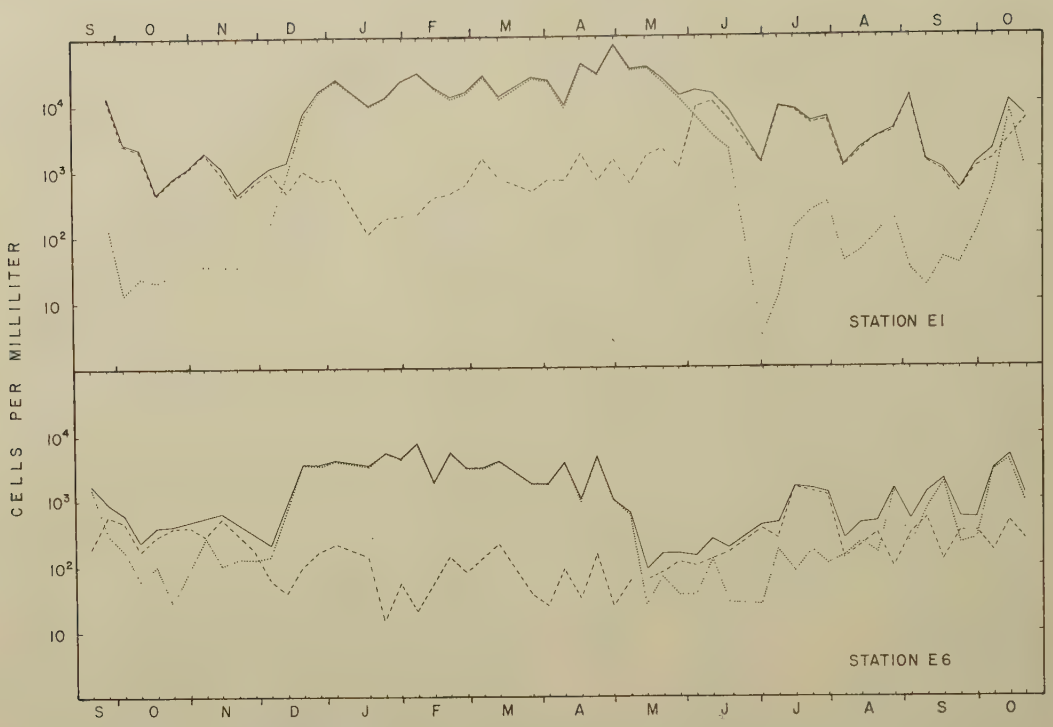

FIG. 2. Seasonal cycle of phytoplankton at the head (upper graph, Station E1) and at the foot (lower graph, Station E6) of the East Passage, 1955–56. Dotted line = diatoms, dashed line = flagellates, solid line = total population.

lower Bay; therefore it was not included in the averages.) While mean concentrations in the two passages are about the same, both diatoms and flagellates are more than twice as abundant in the upper than in the lower Bay during all phases of the cycle, with a single exception: in the fourth season diatoms in the lower Bay outnumber those in the upper Bay. Considering the full cycle, the upper Bay is more than three times as rich as the lower, in both diatoms and flagellates.

Figure 2, depicting the complete annual cycles at the head and at the foot of the East Passage, illustrates some features of the growth curve which have not been brought out above, such as the short-term changes in abundance and the rates of increase and decrease.

Species composition

A list of species identified will be found in the Appendix. Two elements in the population are so outstanding in numbers and frequency of occurrence as to deserve immediate mention: "microflagellates" and *Skeletonema costatum*.

The microflagellates include unidentified species apparently belonging to *Chilomonas*, *Cryptomonas*, *Rhodomonas*, and *Massartia* ("gymnodinioid arrowhead" of Smayda 1957) and others not identified to genus. Some are pigmented, others colorless, and all are less than 15 μ in greatest dimension. This group of forms is ubiquitous, is represented in every week of the year, and it comprises most of the flagellate population except during the temporary blooms of certain dinoflagellates and the cryptophycean *Olisthodiscus luteus*. Such blooms merely swell the total numbers rather than replace the microflagellates. Owing in part to its complexity, this category is relatively constant in numerical strength, changing slowly and steadily from winter minimum to summer maximum to winter minimum. Smayda (1957) noted a cyclic periodicity in the numbers of these forms, with a period

of about three weeks in his own data and of two weeks in Ferrara's. In Figure 2 similar fluctuations are suggested in parts of the flagellate curves.

The diatom *Skeletonema costatum* appears in the great majority of samples and is second only to the microflagellates in frequency of occurrence. Numerically it is by far the most important species. For the eight-month period from early summer to late winter, Ferrara (1953) in the upper Bay and Smayda (1957) in the lower Bay have calculated that this species amounts to 80% of the total population. From the present data it is safe to estimate that this approximate proportion holds for the full cycle. *Skeletonema* dominates the population for most of the year, and the seasonal changes in its abundance largely account for the dominance of the diatoms in the first and third periods, the dominance of the flagellates in the second and fourth (in default of this species), and the gross cyclic changes in the total standing crop.

Spatial differences in species composition. The degree of qualitative variation from one part of the Bay to another can best be seen in the 1955–56 series. For purposes of regional comparison, the Bay is divided into four areas, with Stations W2 and W5 representing the upper West Passage, Stations W8 and W9 the lower West Passage, Stations E1 and E2 the upper East Passage, and Stations E3 and E6 the lower East Passage. The frequencies of occurrence of each species in these four areas during the 1955–56 cycle have been contrasted in a four-fold contingency table, testing for significance at the 5% level. Table 9 lists the species that occurred with significantly greater frequency in each of the four areas than in one or more of the other quarters. The two parts of the Bay most distinctive in species composition are the highly estuarine upper West Passage, with a flora characterized by certain dinoflagellates, and the lower East occupied by relatively coastal water distinguished by seven diatoms, one dinoflagellate, and one silicoflagellate. Comparisons of mean frequencies for the two upper quarters versus the two lower quarters show *Peridinium trochoideum* in significantly greater frequency in the upper Bay than in the lower, and *Rhizosolenia stolterfothii* preferring the lower Bay to the upper. No contrasts between the East and West Passages reached the 5% level of significance.

TABLE 9. *Species occurring with significantly greater frequency in each of the four quarters of the Bay than in one or more of the other quarters, 1955–56*

Upper West Passage
Gymnodinium nelsoni
Peridinium trochoideum
Peridinium spp.
Goniaulax sp.
Lower West Passage
Chaetoceros danicus
Upper East Passage
Amphiprora sp.
Peridinium trochoideum
Lower East Passage
Rhizosolenia styliformis
Rhizosolenia stolterfothii
Corethron hystrix
Leptocylindrus danicus
Thalassionema nitzschioides
Gyrosigma sp.
Chaetoceros didymus
Ceratium lineatum
Distephanus speculum

If we consider only the "dominant" species, defined as those accounting for 5% or more of any sample, the significant regional contrasts are: *Leptocylindrus danicus* occurring more frequently as a dominant in the lower than in the upper Bay, and *Peridinium trochoideum* and *Olisthodiscus luteus* in the upper West Passage more frequently than in other quarters.

With few exceptions the species mentioned above and in Table 9 are customarily classed as neritic. *Corethron hystrix, Rhizosolenia styliformis,* and (by some writers) *Rhizosolenia stolterfothii*—all characteristic of the lower East Passage—are considered oceanic. Other species listed as typical of the lower East Passage and not usually termed neritic are *Ceratium lineatum* which, inferring from Lebour's (1925, p. 145) and Schiller's (1937, p. 373) statements, is oceanic, and *Distephanus speculum,* described by Gemeinhardt (1930, p. 62) as euryhaline and very broadly distributed. With regard to the species that distinguish the flora of the upper West Passage, *Peridinium trochoideum* is previously reported as thriving in estuarine conditions (Braarud 1945), and Conrad and

Kufferath (1954, p. 147) list *Olisthodiscus luteus* as a fresh and brackish water form.

Seasonal differences. *Skeletonema costatum*, microflagellates, and *Chaetoceroa* spp. are the only forms that regularly occurred as dominants the year round. In all or most years of the study, during the first and third seasons *Skeletonema* has been the most frequent dominant with microflagellates next; in the second and fourth seasons, microflagellates have led in frequency of dominance with *Skeletonema* a close second.

Other species always or usually occurring as dominants in more than one season are: *Leptocylindrus danicus* in the first, third, and fourth seasons, *Leptocylindrus minimus* in the first and second, and *Peridinium trochoideum*, *Thalassiosira nana*, *Nitzschia seriata*, and *Gyrodinium* spp. in the second and third.

The dominant species that distinguish the four seasons are as follows:

Season 1: *Detonula cystifera* and *Thalassiosira nordenskioldii* always dominants, and never so in other seasons; *Peridinium triquetrum* and *Thalassionema nitzschioides* dominants in most years.

Season 2: *Olisthodiscus luteus* and *Gymnodinium* spp. dominants every year, *Prorocentrum gracile* and *Mesodinium* sp. in most years.

Season 3: *Thalassiosira gravida* and *Asterionella japonica* dominants in most years.

Season 4: *Rhizosolenia fragilissima* dominant in most years.

In addition to the cyclic recurrence of dominant forms, there are three variables in the character of the population that show consistent seasonal differences. These are the number of species represented in the Bay, the rate of change in species composition from each week to the next, and the heterogeneity of the Bay plankton (defined as the percentage of species that are present in one quarter only). With regard to these, the four seasons compare thus:

species represented, $3 > 4 > 2 > 1$
rate of change, $4 > 3 > 2 > 1$
heterogeneity, $4 > 3 > 2 > 1$

During the course of the annual cycle, qualitative diversity and temporal and spatial variability increase from the first season to the third and fourth. The winter and early spring period, with its sustained diatom flowering, is marked by relative paucity of species, slow qualitative change, and regional homogeneity. As the cycle advances there is a progressive increase in diversity, in rate of change, and in qualitative differentiation of regional floras, these tendencies reaching maxima in late summer and autumn.

Relation of dominance to temperature. In an attempt to reveal temperature preferences of individual species, each instance of dominance has been plotted against the prevailing temperature, with the data grouped by 1° intervals. Since more samples were taken at some temperatures than at others, a plot of the raw data would give a distorted picture of temperature preferences. The frequency of dominance in each temperature interval has therefore been multiplied by a weighting factor derived by dividing the number of observations made in the modal temperature interval by the number of observations made in the given temperature interval. Each weighted frequency thus represents the number of instances in which the species was a dominant as a percentage of the total number of samples taken at the particular temperature. The weighted frequencies of dominance, plotted against the prevailing temperatures, are shown in Figure 3 for the 12 species or entities that occurred most frequently as dominants. (*Chaetoceros* spp. and *Gymnodinium* spp., which actually ranked third and tenth in frequency, are omitted because they are combinations of species; microflagellates, though also an artificial category, are included as they constitute the most frequently dominant entity.) Most of the weighting factors are below 2. Owing to the small number of samples collected at temperatures below 0°C and above 24°C, the weighting factors for the temperature intervals beyond these points exceed 4. The indicated preferences for these extremes of temperature are therefore less reliable than most of the data, but the only results thus affected are, at the lower end of the temperature scale, the first two bars in the *Skeletonema* histogram, and at the upper end, the last bar for *Thalassiosira nana*, the last bar for *Prorocentrum gracile*, and the last three bars for *Peridinium trochoideum*.

Microflagellates and *Skeletonema costatum*

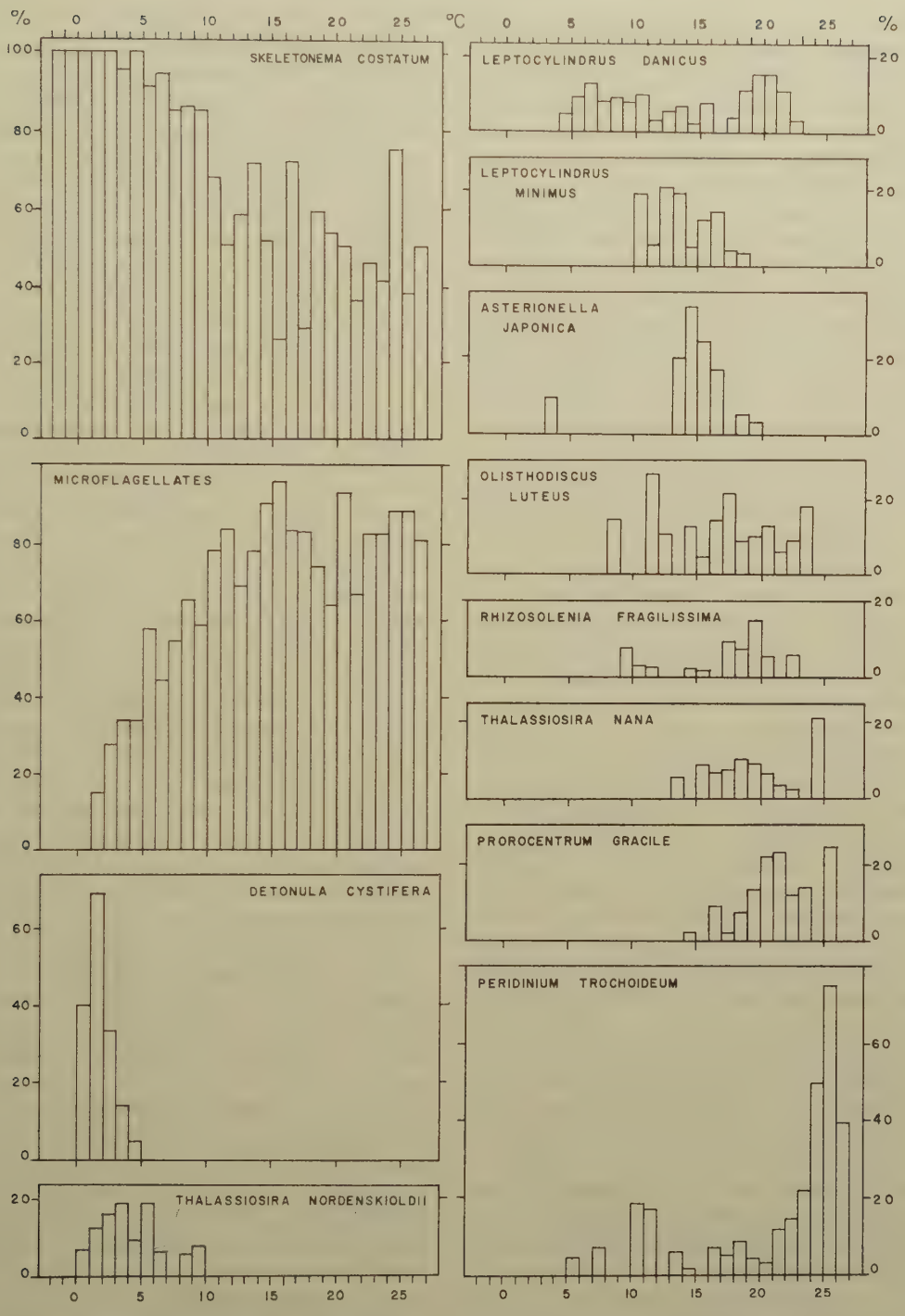

FIG. 3. Weighted frequencies of dominance of various species versus temperature by 1°C intervals.

are the most eurythermal dominants in the population, and their patterns of temperature distribution are complementary. Whereas *Skeletonema* seems to prefer the colder water, at temperatures below 10°C the incidence of dominance of microflagellates decreases steadily, and they never were dominant below 1°C. Of the remaining species figured, some appear to be more or less temperature indifferent, as judged by their ability to dominate the population over a wide range of temperatures, *e.g.*, *Peridinium trochoideum* (5.0–26.9°C), *Leptocylindrus danicus* (4.0–22.9°), and *Olisthodiscus luteus* (8.0–23.9°). Others are evidently much more restricted as dominants by temperature: *Detonula cystifera*, for example, shows a decided preference for the narrow range 0–4.9°C. While not enough is known about the biology of any of these species to account for their seasonal occurrence, data of the type presented in Figure 3, supplemented by laboratory observations under controlled conditions, should eventually explain the role of temperature in seasonal succession and distinguish between its direct and indirect effects.

Frequencies of dominance have also been plotted against prevailing salinities, but no clear correlations were revealed. This is probably explained by the fact that most salinity values fell in a limited range. Although the extremes were 18.66 and 32.05‰, more than two thirds of the values were between 28.50 and 31.50‰.

Parts of the sampling program reported here duplicate the work of others, carried out independently at the same localities during the same periods and using the same methods. Sampling at Station W3 (July–November 1952) duplicates studies by Ferrara (1953), and the observations at Stations W7 and W9 parallel those of Smayda (1957, his Stations I and II) from June to November 1954. Comparisons of the curves (not reproduced here) show excellent agreement.

DISCUSSION

Perhaps the most salient feature of the phytoplankton of Narragansett Bay is its high mean level of abundance as compared with New England coastal waters. The superiority of the Bay standing crops both in cells per unit volume and in cells beneath a unit area of sea surface has been clearly brought out by Smayda (1957). For the period June–February in a single cycle he gives 6,700 cells/ml as the overall mean for his three stations in the lower Bay, and quotes 10,000 cells/ml for a similar period for Ferrara's station in the upper Bay. We now have figures for a full cycle (1955–56, Table 8): 3,106 cells/ml for the lower Bay (four stations), and 10,209 cells/ml for the upper Bay (four stations). Smayda's lower Bay average is heavily influenced by the high concentrations at his "ultraestuarine" Station I. This explains in part the disparity between his average and mine. The composite average from three full cycles for the Bay as a whole (derived in Table 7) is 6,117 cells/ml, as compared with reported mean concentrations in New England coastal waters ranging from about 23 cells/ml in Vineyard Sound (Lillick 1937) to 2,500 cells/ml in Long Island Sound (Conover 1956). It should be pointed out, however, that in all of these studies outside of the Bay the samples were "preserved" with formalin, with the consequent destruction of naked flagellates. A fair comparison would probably be one between Lillick's and Conover's averages on the one hand, and on the other the average for the Bay less the numbers of microflagellates, but even if we discount *all* of the flagellates, Table 7 shows that the mean concentration in Narragansett Bay (diatoms only) is 5,306 cells/ml, or still twice as great as the highest average recorded for the entire population in nearby coastal waters.

Six of the most important species recurring annually as dominants in Narragansett Bay (under section on seasonal differences) are not listed as dominants, similarly defined, by Riley (1952) for Block Island Sound nor by Conover (1956) for Long Island Sound. These are: *Thalassiosira nana*, *Detonula cystifera*, *Peridinium triquetrum*, *Olisthodiscus luteus*, *Prorocentrum gracile*, and *Mesodinium* sp. and, as previously noted, Riley and Conover were not able to estimate the numbers of micro-

flagellates, the most persistent dominant element of the Bay plankton. Even lacking such data, one may conjecture that the phytoplankton of Narragansett Bay, especially in the upper area where the flagellates are most successful, is qualitatively somewhat intermediate between that of the coastal water and the populations of salt and brackish coastal ponds. One of these ponds, fed by a river and emptying into Vineyard Sound about 40 miles to the east of Narragansett Bay, has been studied by Hulburt (1956), who described a plankton flora marked by the variety and richness of its flagellate constituents.

The annual cycle in Narragansett Bay is perhaps unique in one respect—the length of the winter-spring diatom flowering (season 1). A steady increase begins as early as mid-November, and the maximum concentrations are reached sometime between late December and the end of January and are sustained until May. This is in contrast with the course of events in Block Island Sound (Riley 1952) and Long Island Sound (Conover 1956), where a sudden increase in February leads to a sharp peak, followed by an immediate decline to low levels in late March. A sequence somewhat intermediate between these and the Narragansett Bay winter picture was described by Riley (1941) for a shore station in Long Island Sound, where the diatom flowering began in January, reached large proportions by late February and declined in April. From a study of the relative abundance of forms in net hauls, Fish (1925) concluded that the diatom flowering at Woods Hole, Massachusetts, begins in November, reaches a maximum in December, and continues until March—a winter season that, although not quantitatively described and terminating earlier, bears some resemblance to that in Narragansett Bay. The unusual duration of the winter-spring diatom flowering in the Bay largely accounts for the high annual mean.

Smayda (1957) has advanced an explanation for the early start of this flowering. He reasons that, whereas in deeper waters such as Block Island Sound a burst of growth cannot occur until the population is adequately contained in the surface layers by a degree of stratification, the shallowness of Narragansett Bay and its low rate of exchange with the sea combine to produce the "containment" required for flowering without the need of stabilization of the water mass. Turbulence may be continually bringing parts of the population down to poorly illuminated levels, but it returns them to the upper layers soon enough to allow a slow but steady growth. In addition, it is constantly replenishing the supply of nutrients at the surface, and its net effect is to prolong the period of augmentation.

Studies by Hicks (1959) provide a more critical appraisal of the effect of water exchange with Rhode Island Sound. This exchange has, of course, two elements: tidal and nontidal. It is to the advantage of the Bay plankton that the nontidal drift or net seaward movement is not excessive. On the other hand, the tidal activity of Narragansett Bay is considerable (as compared, for example, with Chesapeake Bay), and this is the major generating force of the turbulence which so favors phytoplankton growth.

Extending Smayda's thought to the period for which he had no data, *i.e.*, after February, one can account for the maintenance of the flowering after it reaches peak abundance—a plateau from January to May—by the same mechanism: a turbulence that, in effect, provides the cells with nutrients and yet does not deny them the light. This continues until significant stratification occurs in April (Hicks, personal communication). Thereafter, the surface populations are maintained by the unreplenished nutrient stores in the upper layers; when these are exhausted in May, there is a sudden and precipitous decline.

The early start of population growth, the prolonged period of increase, and its continued flowering into the spring thus appear to be related to the average shallowness of the Bay combined with turbulence and a moderate nontidal drift. This explanation would lead one to expect that the flowering would begin earlier in the shallow West Passage than in the deeper East Passage, and that it would begin first in the shallow

upper reaches and then progressively seaward in the deeper lower Bay. Conversely, in the spring one should look for an earlier termination of the flowering in the deeper seaward areas, where stratification sooner prevents effective mixing to the bottom than in the shallower upper areas where daily tidal mixing is still effective. These expectations are generally realized in the one year (1955–56) for which we have adequate information: Table 2 shows that the flowering began, on the average, earlier in the West Passage than in the East, that in the East Passage its initiation came progressively later seaward, and that in the spring it terminated generally sooner in the East than in the West Passage and in both passages first at the seaward end.

The other major features of the annual cycle are similar to those in neighboring areas. The time of occurrence, magnitude, and duration of the summer flagellate maximum (corresponding to our season 2) and the diatom bloom that follows (season 3) appear from the literature to be as unpredictable in adjacent waters as they are in Narragansett Bay. For example, the summer diatom maximum was noted in July and August at Woods Hole by Fish (1925), in August in Vineyard Sound (Lillick 1937), in July in Block Island Sound (Riley 1952), while in Long Island Sound it occurred in September–October of 1938, at the end of July 1939 (Riley 1941), in June–July 1952 and in October 1953 (Conover 1956). Smayda has indicated that the summer diatom burst in Narragansett Bay does not appear to depend on the destruction of the thermocline. If by this is meant the annual breakdown of stratification by a general cooling of the surface waters and overturn, the dates of occurrence cited above suggest that Smayda's statement applies to a larger area. All along the southern New England coast the secondary diatom flowering is typically a summer event and frequently takes place before water temperatures have dropped significantly. Vertical mixing therefore appears to be less important here than in areas where this maximum (termed the autumnal flowering) must await the major annual breakdown of stratification in the fall.

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APPENDIX

List of species, and their occurrence by month

An × indicates occurrence during the month in any of the years in which samples were taken.

J	F	M	A	M	J	J	A	S	O	N	D	
												Diatoms
												a) **Centric**
—	—	—	—	—	—	—	×	—	×	—	—	*Bacteriastrum* sp.
—	×	—	—	—	—	—	—	×	×	—	—	*Biddulphia aurita* (Lyngbye) Brébisson and Godey
—	—	—	—	—	—	—	×	—	—	—	—	*Chaetoceros affinis* Lauder
×	×	—	—	—	—	—	×	×	×	×	×	*Chaetoceros curvisetus* Cleve
×	×	×	—	—	×	×	×	×	×	—	—	*Chaetoceros danicus* Cleve
—	×	×	×	×	—	—	×	×	×	×	—	*Chaetoceros decipiens* Cleve
×	×	×	—	×	×	×	×	×	×	×	—	*Chaetoceros didymus* Ehrenberg
×	×	—	×	×	×	—	—	—	—	×	×	*Chaetoceros gracilis* Schütt
—	—	×	×	×	—	—	—	—	—	—	—	*Chaetoceros laciniosus* Schütt
×	×	—	—	—	—	×	×	—	×	×	×	*Chaetoceros lorenzianus* Grunow
×	×	×	—	—	—	×	—	×	—	—	×	*Chaetoceros similis* Cleve
—	—	—	—	—	×	×	×	—	—	—	—	*Chaetoceros simplex* Ostenfeld
—	—	—	—	—	—	—	×	×	—	—	—	*Chaetoceros socialis* Lauder
—	—	—	—	—	—	×	×	×	×	—	—	*Chaetoceros teres* Cleve
—	—	—	—	×	—	—	—	—	—	—	—	*Chaetoceros tortissimus* Gran
×	×	×	×	×	×	×	×	×	×	×	×	*Chaetoceros* spp.
×	×	—	—	—	—	—	×	×	×	×	×	*Corethron hystrix* Hensen
×	×	×	×	×	×	×	×	×	×	×	×	*Coscinodiscus* spp.
×	×	×	×	—	—	—	—	—	—	—	×	*Detonula cystifera* (Cleve) Gran
×	—	—	—	—	—	—	—	×	×	×	×	*Ditylum brightwellii* (West) Grunow
—	—	—	—	—	—	—	—	—	×	—	—	*Eucampia zoodiacus* Ehrenberg
×	×	—	—	—	—	×	×	—	×	×	—	*Guinardia flaccida* (Castracane) Péragallo
—	×	—	—	—	—	—	—	×	×	—	—	*Hemiaulus sinensis* Greville
×	×	×	×	×	×	×	×	×	×	×	×	*Leptocylindrus danicus* Cleve
×	×	×	×	×	×	×	×	×	×	×	—	*Leptocylindrus minimus* Gran
—	—	—	—	—	×	—	—	×	×	×	—	*Lithodesmium undulatum* Ehrenberg
×	×	×	×	×	—	—	×	×	×	×	×	*Melosira sulcata* (Ehrenberg) Kützing
—	—	—	—	—	—	×	×	—	×	×	×	*Melosira* sp.
—	—	—	—	—	×	×	×	×	×	×	×	*Rhizosolenia delicatula* Cleve
×	×	×	×	—	—	—	—	—	—	—	—	*Rhizosolenia faeroense* Ostenfeld
—	—	—	—	×	×	×	×	×	×	—	—	*Rhizosolenia fragilissima* Bergon
—	—	—	—	—	—	—	—	—	×	—	—	*Rhizosolenia hebetata* form *semispina* (Hensen) Gran
×	×	×	×	×	×	×	×	×	×	×	×	*Rhizosolenia setigera* Brightwell
—	—	—	—	—	—	—	×	—	×	×	×	*Rhizosolenia stolterfothii* Péragallo
×	×	×	—	—	—	×	×	×	×	×	×	*Rhizosolenia styliformis* Brightwell
—	×	—	—	—	—	—	—	×	×	—	—	*Rhizosolenia* sp.
—	—	×	×	×	—	—	—	—	—	—	—	*Schröderella delicatula* (Péragallo) Pavillard
×	×	×	×	×	×	×	×	×	×	×	×	*Skeletonema costatum* (Greville) Cleve
—	—	—	—	—	—	—	—	×	×	×	×	*Stephanopyxis* sp.
×	×	—	—	×	—	×	×	×	×	×	×	*Thalassiosira decipiens* (Grunow) Jørgensen
—	—	—	—	×	×	×	×	×	×	×	—	*Thalassiosira gravida* Cleve
—	—	—	—	—	—	×	×	×	×	—	—	*Thalassiosira nana* Lohmann
×	×	×	×	×	—	—	—	—	—	—	×	*Thalassiosira nordenskiöldii* Cleve
—	—	—	—	—	—	×	—	×	×	—	—	*Thalassiosira rotula* Meunier
×	×	—	—	—	—	×	×	×	×	×	—	*Thalassiosira* sp.
												b) **Pennate**
—	—	—	—	—	×	×	×	—	×	×	—	*Achnanthes longipes* Agardh
×	×	×	×	×	×	—	×	×	×	×	×	*Amphiprora* sp.
×	×	×	×	×	—	×	—	×	×	×	×	*Asterionella japonica* Cleve
—	—	×	—	—	—	—	—	—	—	—	×	*Fragilaria* sp.
—	—	—	—	—	×	×	×	×	×	×	×	*Grammatophora marina* (Lyngbye) Kützing
×	×	—	—	×	—	×	×	×	×	×	×	*Gyrosigma* spp.
—	×	—	×	×	×	×	×	—	×	×	×	*Licmophora* sp.
×	×	×	×	×	×	×	×	×	×	×	×	*Navicula* spp.
×	×	×	×	×	×	×	×	×	×	×	×	*Nitzschia closterium* (Ehrenberg) W. Smith
×	—	—	—	—	—	—	×	×	×	×	—	*Nitzschia longissima* (Brébisson) Ralfs
×	×	×	×	×	×	×	×	×	×	×	×	*Nitzschia reversa* W. Smith
×	×	×	×	×	×	×	×	×	×	×	×	*Nitzschia seriata* Cleve

J	F	M	A	M	J	J	A	S	O	N	D	
												b) **Pennate**
—	—	—	×	—	—	×	×	×	×	×	—	*Rhabdonema adriaticum* Kützing
×	×	—	—	—	×	×	—	×	×	×	—	*Striatella unipunctata* (Lyngbye) Agardh
—	—	—	—	—	—	—	×	—	—	×	—	*Surirella* sp.
—	×	—	×	—	×	×	—	—	×	×	—	*Thalassiothrix frauenfeldii* Grunow
—	×	×	×	—	—	—	—	—	—	—	—	*Thalassiothrix longissima* Cleve and Grunow
×	×	×	×	×	×	×	×	×	×	×	×	*Thalassionema nitzschioides* Grunow
												Dinoflagellates
—	—	×	—	—	—	—	×	×	—	—	—	*Amphidinium* sp.
—	—	—	—	—	×	—	×	—	×	—	—	*Ceratium fusus* (Ehrenberg) Dujardin
—	—	—	—	×	×	×	×	×	×	—	—	*Ceratium lineatum* (Ehrenberg) Cleve
—	—	—	—	×	×	×	×	—	×	—	—	*Ceratium longipes* (Bailey) Gran
—	—	—	—	×	×	—	—	—	—	—	—	*Ceratium minutum* Jörgensen
—	—	—	—	—	—	—	—	×	—	—	—	*Ceratium tripos* (O. F. Müller) Nitzsch
—	×	—	×	×	×	×	×	×	×	×	—	*Dinophysis acuminata* Claparede and Lachman
—	—	—	×	×	—	—	—	—	—	—	—	*Glenodinium lenticula* (Bergh) Schiller
×	—	—	—	—	—	×	—	×	×	×	×	*Goniaulax* sp.
—	—	—	—	—	—	×	×	×	×	—	—	*Gymnodinium nelsoni* Martin
×	×	×	×	×	×	×	×	×	×	×	×	*Gymnodinium* spp.
×	×	×	×	×	×	×	×	×	×	×	×	*Gyrodinium* spp.
×	×	×	×	×	×	×	×	×	×	×	×	*Massartia* sp.
—	—	—	×	×	×	×	—	×	—	—	×	*Oxytoxum* sp.
—	—	—	—	—	—	—	—	×	—	—	—	*Peridinium conicum* (Gran) Ostenfeld and Schmidt
—	—	—	×	×	—	—	—	—	—	—	—	*Peridinium depressum* Bailey
—	—	—	—	×	—	—	—	—	—	—	—	*Peridinium excentricum* Paulsen
×	—	—	×	—	—	—	—	—	—	—	—	*Peridinium Granii* Ostenfeld
—	—	—	×	×	×	—	—	—	×	—	—	*Peridinium minusculum* Pavillard
—	—	—	×	—	—	—	—	—	—	—	—	*Peridinium minutum* Kofoid
—	—	—	—	—	—	—	—	—	—	×	—	*Peridinium Steinii* Jörgensen
—	—	×	×	×	×	×	—	—	×	—	—	*Peridinium triquetrum* (Ehrenberg) Lebour
×	×	×	×	×	×	×	×	×	×	×	×	*Peridinium trochoideum* (Stein) Lemmermann
×	×	×	×	×	×	×	×	×	×	×	×	*Peridinium* spp.
—	—	—	—	—	—	—	×	×	×	—	—	*Polykrikos* sp.
—	—	—	—	—	×	×	×	×	×	×	—	*Prorocentrum gracile* Schütt
—	—	—	—	—	×	—	×	—	—	—	—	*Prorocentrum micans* Ehrenberg
—	—	—	—	×	×	×	×	×	×	×	×	*Prorocentrum scutellum* Schroeder
—	—	—	—	—	—	—	—	×	×	—	—	*Pyrocystis* (*Dissodinium*) *lunula* Schütt
												Other algae
×	×	×	×	×	×	×	×	×	×	×	×	*Chilomonas* sp. (Cryptophyceae)
×	×	×	×	×	×	×	×	×	×	×	×	*Cryptomonas* sp. (Cryptophyceae)
—	—	—	—	×	×	×	×	×	×	×	×	*Olisthodiscus luteus* Carter (Cryptophyceae)
—	—	—	—	—	—	×	×	×	×	—	—	*Rhodomonas* sp. (Cryptophyceae)
—	—	—	—	—	×	×	—	—	×	×	—	*Dictyocha fibula* Ehrenberg (Silicoflagellata)
×	×	×	—	×	×	×	×	×	×	×	×	*Distephanus speculum* (Ehrenberg) Haekel (Silicoflagellata)
×	—	—	—	×	×	×	×	×	×	×	×	*Ebria tripartita* (Schumann) Lemmermann (Silicoflagellata)
×	—	×	—	—	×	×	×	×	×	×	—	*Euglena* sp. (Euglenophyceae)
—	—	×	×	—	—	—	—	—	—	—	—	*Eutreptia* sp. (Euglenophyceae)
×	—	—	×	×	×	×	×	×	×	×	—	*Pyramimonas* sp. (Chlorophyceae)
—	—	—	—	—	—	—	—	×	×	—	—	*Scenedesmus* sp. (Chlorophyceae)
												Ciliates
—	—	—	—	—	—	—	×	×	×	—	—	*Codonella* sp.
×	×	×	×	×	×	×	×	×	×	×	×	*Mesodinium* sp.
×	×	×	×	×	×	×	×	×	×	×	×	*Tintinnopsis* sp.
×	—	×	×	—	×	×	×	×	×	×	×	*Tintinnus* sp.

Evidence of Internal Wave Activity in Cayuga Lake, New York[1]

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ABSTRACT

Temperature observations from a station near the southern end of Cayuga Lake, New York, reveal variations in the depths of the isotherms which suggest the presence of temperature seiches, or internal waves. The theoretical period of oscillation of a uninodal internal wave, based on summer temperature conditions of the lake, ranges between 55 and 58 hours. A sequence of temperature observations at the level of the metalimnion for the first eight days of August, 1951, are presented, and the observed variations are in accord with the theoretical variations. The winds during the time under consideration were reinforcing and occurred in synchrony with the seiche movements, producing an amplitude in excess of 20 meters which is about twice the normal amplitude. Observations of surface currents and temperatures give supporting evidence for the presence of internal wave activity.

INTRODUCTION

Examination of the temperature data collected from Cayuga Lake, New York, from 1950 through 1953 reveals vertical variations that suggest the presence of temperature seiches or internal waves. Some of these data can be used to estimate the period of oscillation.

Cayuga Lake (Fig. 1) is one of the long and deep Finger Lakes of central New York State. It is 38 miles long, has a maximum width of 3.5 miles, and is 434 feet deep. The deepest sounding is near the geographical center of the basin. The main axis of the lake, lying in a northwest to southeast direction in line with the prevailing northwest winds, gives the lake an extensive fetch. The morphometry of the basin is simple with but few irregularities of shoreline. Limnological studies of this lake have been presented by Birge and Juday (1914, 1921), Burkholder (1931).

Temperatures were collected from a 100-meter-deep sampling station situated south of Taughannock Point, about ten miles from the southern end of the lake (Fig. 1). The 1950 data were collected by means of a bathythermograph calibrated to a depth of 200 feet (62 meters), and beginning in 1951, a 450-foot (137 meters) instrument loaned by the Woods Hole Oceanographic Institution was also used. Surface temperatures were collected as routine procedure, and several vertical temperature series were obtained with a reversing thermometer to use as additional control. Sampling dates were irregularly spaced, although an attempt was made to obtain at least one bathythermogram weekly during the summer seasons.

VARIATIONS IN TEMPERATURE CONDITIONS OBSERVED IN CAYUGA LAKE

A graph of the summer isotherms plotted against time revealed considerable fluctuation of the temperatures with respect to depth. Figure 2 illustrates the variations in depth of the 15° isotherm, the 10° isotherm which was included in the thermal gradient, and the 6° isotherm which was near the top of the hypolimnion. The period covered in this figure is from June 9 through September 7, 1951. Similar fluctuations of the profundal 5° isotherm were observed.

Temperature profiles also indicated major changes in character during short periods of time. Figure 3 illustrates differences observed in the vertical temperature distribution from the Taughannock station for three

[1] The temperature observations reported on here were collected during a general survey of Cayuga Lake during 1950 through 1953 by D. C. Chandler, A. S. Bradshaw, and the author. Much of the equipment used in this study was provided by the Elizabeth Thompson Science Fund. The critical reading of the manuscript by John Ayers is appreciated.

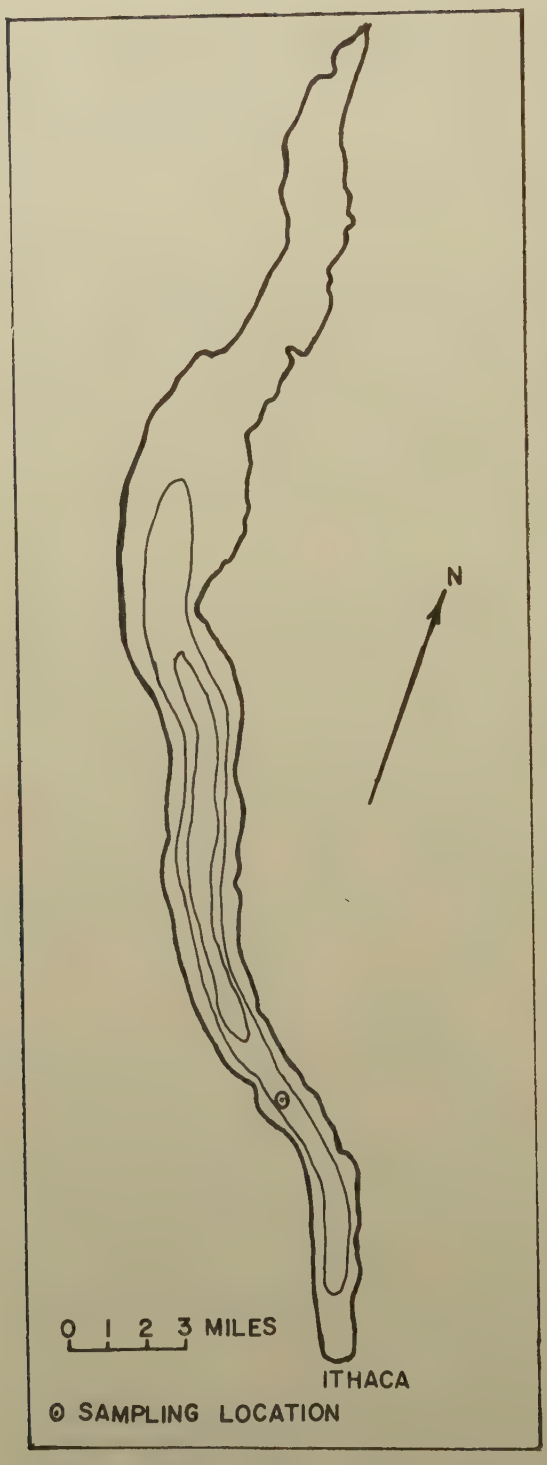

FIG. 1. Map of Cayuga Lake, New York, showing the location of the Taughannock sampling station. Contour intervals are 200 feet.

days in August 1951. On August 20 there was a shallow epilimnion and a continuous thermal gradient extending from 5 meters to a depth of about 40 meters. Three days later the character of the profile had changed so that there was a well-defined epilimnion to 15 meters with a moderate metalimnion between 15 and 22 meters. On August 29 the temperature profile was of an intermediate configuration.

These variations suggest temperature seiches, or internal waves, which become established as the result of wind action. The wind conditions, expressed as the total daily wind movement in miles, for the last half of August are depicted in Figure 3. These wind data, taken from the monthly reports of the U. S. Weather Bureau, were recorded on the Cornell University campus located at the southeastern corner of the lake. High wind activity occurred on August 22, but reasonable calm persisted for the remainder of the month. It is possible that the wind of August 22 initiated a temperature seiche, and that the differences in the temperature distribution between August 23 and 29 are due to internal wave activity.

THE CONCEPT OF INTERNAL WAVES

Temperature fluctuations at the level of the metalimnion have been observed before. The Scottish Lake Survey made a classical pioneer investigation into this phenomenon (Watson 1904, Wedderburn 1907), but little has been done in this country, though Birge (Birge and Juday 1914, p. 556) was keenly aware of it. Recently Mortimer re-examined the subject of internal waves in Lake Windermere, England, and from model tank experiments (1951, 1952a, 1952b). In 1953 Mortimer provided an excellent review of the subject and presented a simple method with nomograms for calculating the theoretical periods of oscillation. Mortimer's papers are recommended for detailed descriptions of this aspect of physical limnology.

The accepted hypothesis recognizes that during times of wind stress the warm surface water is transported with the wind, and is accumulated at the lee end of the lake.

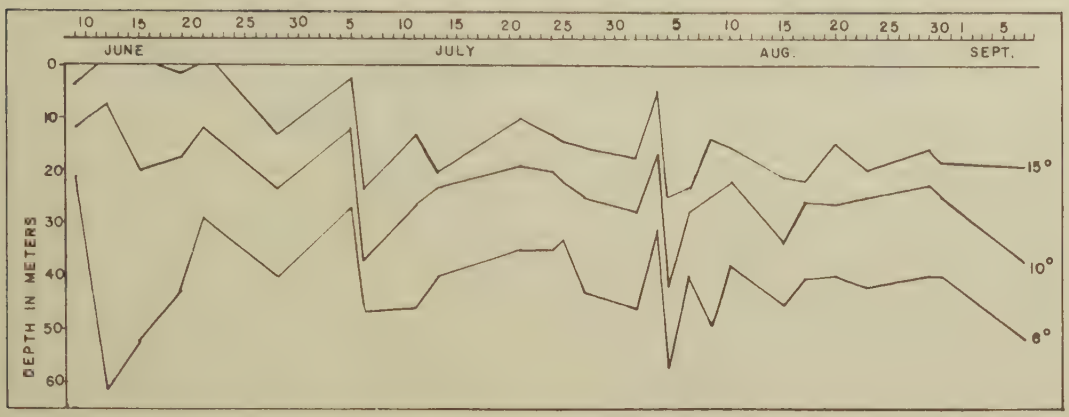

FIG. 2. Fluctuations of the 6°, 10°, and 15°C isotherms as observed from the Taughannock station, Cayuga Lake, from June 9 through September 7, 1951.

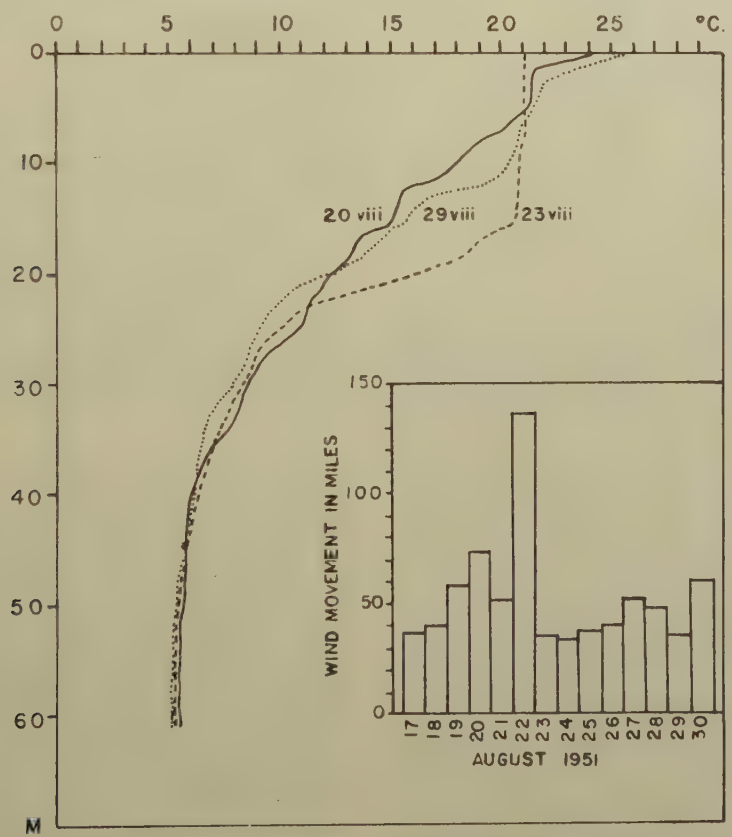

FIG. 3. Temperature profiles observed from Taughannock station, Cayuga Lake, on August, 20, 23, and 29, 1951. The inset diagram presents the total daily wind movement in miles for the two weeks in August that include the dates of temperature observations.

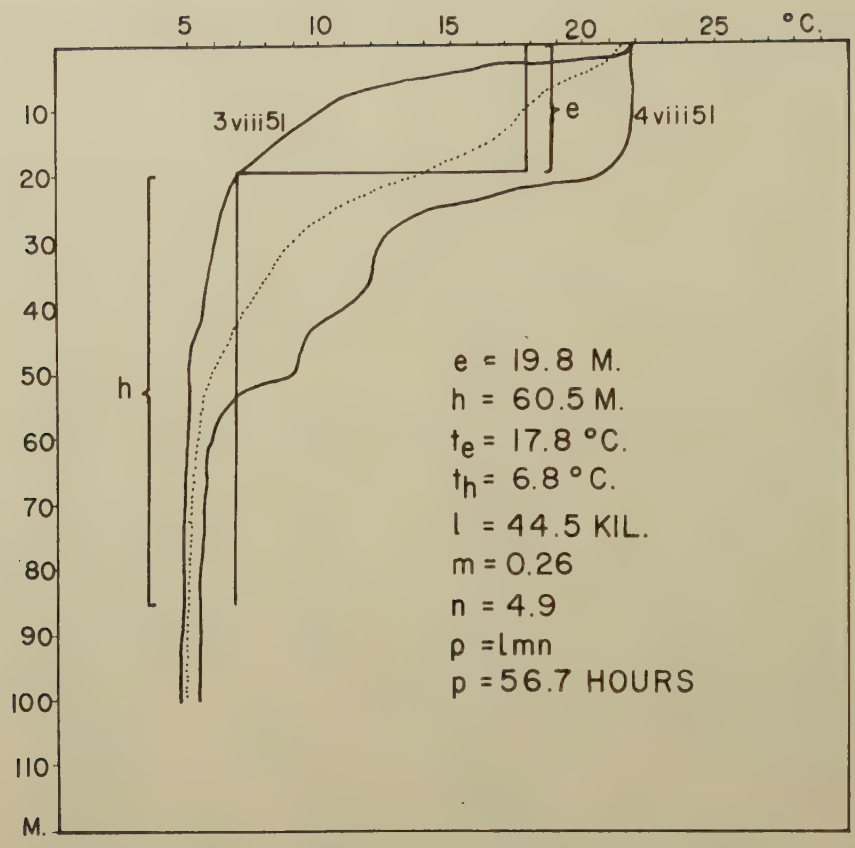

FIG. 4. Temperature profiles for August 3 and 4, 1951, from the Taughannock station, Cayuga Lake. The mean temperature conditions of August 1 through August 8 are represented by the dotted line. The various factors listed are used in calculating the theoretical period of oscillation of a uninodal temperature seiche.

This transport disrupts the hydrostatic equilibrium, and causes an upwelling of the cooler and deeper water at the windward end of the lake, where the isotherms are deflected upward toward the surface.

With the cessation of the disruptive force (the wind) the isotherms begin to move in a pendulous manner. A lake that has become stratified is essentially a two-layered system with less dense fluid over one of greater density separated by a discontinuity layer (metalimnion).[2] When a body of water is displaced from equilibrium by the wind, the discontinuity layer serves as a plane of slip upon which the lighter epilimnial water rides over the hypolimnion. The unequal densities of the two fluids (or parts of the lake) account for the differences in periods observable in the two regions. Readjustment to equilibrium induces a standing wave across the boundary between the two fluids (metalimnion). A seiche of the uninodal type is the most predominant response of a lake to wind (Mortimer 1953).

[2] Mortimer (1953) has found that for all practical purposes, a two-layer theory works satisfactorily without the need to consider the three-layer theory in a discussion of metalimnion seiches.

ANALYSIS OF DATA FOR INTERNAL WAVES

Mortimer (1953) offers a simple means to compute the theoretical period of oscillation of a uninodal internal wave if we are given a representative temperature profile and a bathymetric map of the lake. Correlation of the theoretical with the observed period

is satisfactory if the theoretical computations are based on a temperature profile that represents the mean conditions of the lake during the time considered. Such an ideal profile is approximated by a temperature series taken near the geographic center of the lake, or more specifically, at the nodal center of oscillation. In order to obtain a temperature profile that would approximate the mean conditions during the time interval, hypothetical profiles were plotted from the average temperatures for each depth. This method was found by Mortimer to be satisfactory.

Eleven bathythermograms were obtained during the period from August 1 through August 8, 1951. Two or three temperature recordings were made on each of four of these days. The temperature profiles for two of the eleven temperature records, representing the extreme conditions, are shown in Figure 4. On August 3 there was no definite epilimnion, and a thermal gradient extended between 2 and 10 meters. The next day presented the other extreme with a distinct thermal gradient between 20 and 26 meters and a homogeneous epilimnion. The mean conditions during this period of time, estimated by the average temperature at each depth of the eleven temperature readings, are indicated by the dotted line.

Calculation of the theoretical period is outlined in Figure 4. The mean conditions during this time exhibited a central thermal gradient (depth of steepest slope) at 19.8 meters (e). The mean temperature of the water down to depth e (t_e) was 17.8°C. The mean depth of the lake below 19.8 meters (h) was 60.5 meters, and the mean temperature of h (t_h) was 6.8°C. The length of the medial tract (l) of the lake at depth e was 44.5 kilometers. The values m and n were obtained from Mortimer's nomograms. The theoretical period of oscillation, given by the equation $p = lmn$ is then computed to be 56.7 hours (2.4 days).

The temperatures observed at e are plotted in Figure 5. The five points for August 3 and 4 were sufficiently close together to enable a fragment of a curve to be drawn. It was assumed that point C approximated the uppermost position of the seiche wave (7° at 19.8 meters) and that point G (21° at 19.8 meters) approximated the lowest portion of the wave. The curve $CDEFG$ in Figure 5 was drawn, and, on a basis of similarity and with a cycle of 57 hours, *i.e.*, a distance between similar points of the curve representing 57 hours, was continued in both directions. If internal waves were responsible for the fluctuations and the calculated period is correct, then the observed points should coincide with the constructed curve.

The completed diagram (Figure 5) shows that most of the points do fall on the curve, and it appears logical to conclude that the internal waves were responsible for these temperature variations.

Known wind conditions as recorded on the Cornell campus are depicted in Figure 5 as the square of the velocity observed in miles per hour. The velocities are squared because the stress of the wind on the water surface is proportional to the square of the velocity (Sverdrup *et al.* 1942, p. 490). Winds from the northern quadrants are represented by bars above the line, the length being in proportion to the square of the velocity, while winds from the southern quadrants are drawn below the line. The last several days of July were calm. On July 31 the maximum observed wind velocity was from the southwest at 12 m.p.h. On August 1, with the passing of a cold front, the wind shifted to the northwest attaining velocities to 20 m.p.h. On August 2 the wind shifted to the southwest and 18 m.p.h. The winds returned to the northwest quadrant during the afternoon of August 3 with the passing of another cold front, and subsequently diminished. On August 7 the winds were from the south to 16 m.p.h., associated with another frontal storm.

Since Figure 5 shows the temperature changes at a constant depth (19.8 meters) at the southern end of the lake, an ascending portion of the curve, as at points C through G, represents increasing temperatures at that depth, or, the sinking of isotherms. Conversely, a descending portion of the curve represents decreasing temperatures

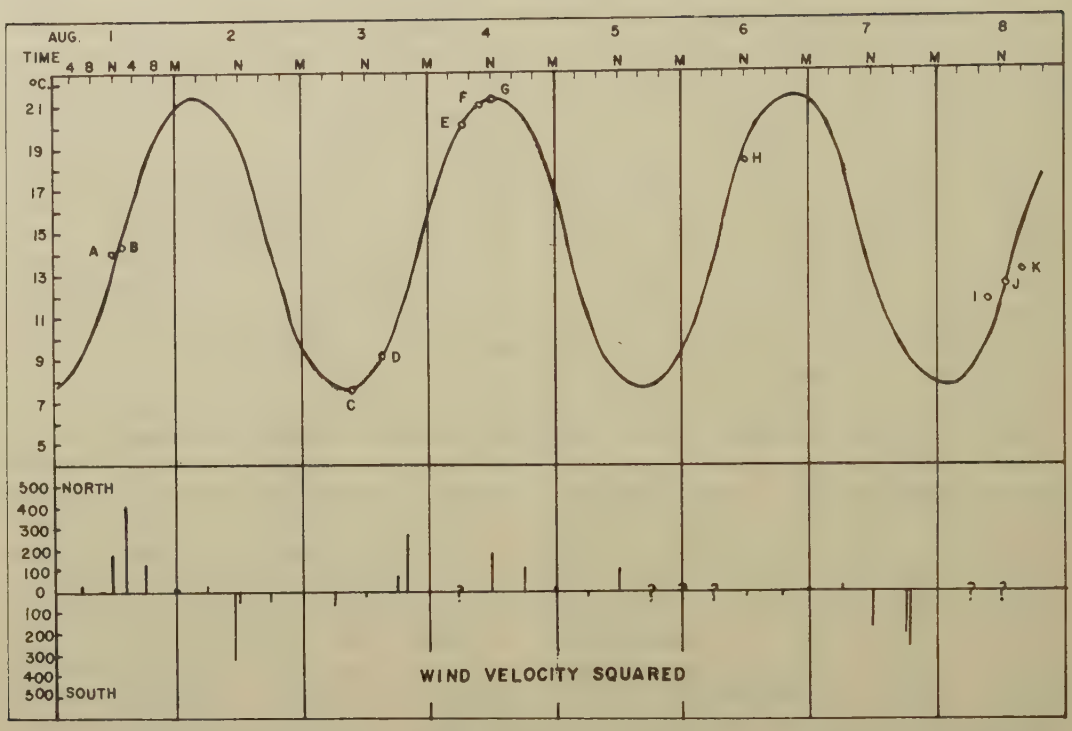

FIG. 5. The observed temperatures of the metalimnion (19.8 meters) at the Taughannock station, Cayuga Lake for August 1 through August 8, 1951 are represented by points *A* through *K*. The curve represents the theoretical temperature conditions at 19.8 meters. Wind conditions are indicated by the bar graph, the length of the bar being proportional to the square of the wind velocity. Bars above the line indicate winds from the northern quadrants, and bars below the line indicate winds from the southern quadrants.

caused by rising isotherms. Since winds from the south induce rising isotherms at that end, south winds occurring when the curve in Figure 5 was descending would have the effect of reinforcing the seiche. Northerly winds would accumulate warm surface water at the southern end of the lake, depress the isotherms there, and reinforce the seiche if they occurred when the curve was ascending. Since the curve at points *A* and *B* is ascending, the northwest winds of August 1 would have reinforced the seiche. On August 2 the isotherms were rising at the southern end of the lake and were being reinforced by the southerly winds of that day. The northwest winds (16 m.p.h.) of August 3 were also reinforcing. The northerly winds of the afternoon of August 4 were damping. The storm of August 7 brought reinforcing southerly winds.

Field notes taken during those days support the concept of internal wave activity. On the morning of August 3 the surface temperature of the lake was 21.1° and quantities of debris and aquatic plants were observed floating on the water, indicating south-end water that had moved north. At 3:20 in the afternoon there was in evidence a strong surface current from the north (with a south breeze)[3], and the surface temperature had decreased to 19.4°C. According to Figure 5, a seiche reversal would have occurred during the forenoon of August 3,

[3] Since the meteorological reports from Cornell included wind conditions for only specific times of day the south breeze referred to here is not included in Figure 5. Mr. Bradshaw and the author became acutely aware of the shifting winds that anticipated the passing of a cold front on this day, and the dramatic reversal of the surface currents. This experience demonstrates the value of taking copious field notes.

and in the afternoon surface water would have flowed into the southern end as indicated by the increasing temperatures at 19.8 meters. The next morning (August 4) the surface current was still from the north. On the afternoon of August 6 the surface water was observed to be slowly flowing from the south. This observation was made just prior to the theoretical reversal of the seiche. Movement of the surface water would anticipate internal seiches. Again, on the morning of August 8, there was a surface current flowing north with a temperature of 17.8°, but in the afternoon the current had reversed itself and the temperature was 22.2°C. Field observations concur with the calculated seiche activity.

DISCUSSION

Stratification in Cayuga Lake is best developed during July and August. In the other months the differences in density between the upper and lower layers of water are small, and as a result the periods of oscillation of internal seiches are too large (100 to 200 hours) for proper analyses. Calculation for the theoretical periods for the summer months of 1950 through 1953 yields a range of 55 to 58 hours, which may be considered normal for Cayuga Lake in summer. Among those lakes whose periods were calculated by Mortimer (1953) this value compares most closely with the 60-hour period in Loch Ness.

Fluctuations shown in Figure 2 indicate normal amplitudes of 7 to 16 meters. These observations were made approximately ten miles from the southern end of the lake, and if an amplitude of 10 meters be considered average at the sampling station, the amplitude would be approximately 15 meters at the southern end. A period of oscillation of 57 hours indicates a vertical movement of water at the rate of 0.3 meters per hour. The example described in this paper had an amplitude in excess of 20 meters, unusually high. During the first three days of August the winds were reinforcing and occurred in complete synchrony with the seiche movements. This combination induced larger than normal amplitudes. The frequency with which the wind activity is in phase with the internal seiche is a matter of conjecture.

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The Hydrography of Barnstable Harbor, Massachusetts[1]

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ABSTRACT

Barnstable Harbor, on the north shore of Cape Cod, Massachusetts, originated from the growth of an offshore barrier bar across an indentation of the coastline. In common with many other East Coast tidal embayments of similar origin it has: 1) low runoff, carried by a few small streams, which together with direct rainfall and groundwater seepage provides a total freshwater acquisition that is small compared to the tidal prism volume; 2) essentially marine internal aquatic environments; and 3) extensive salt marshes drained by tidal creek systems. The hydrography of the harbor is largely determined by the internal arrangement of its shoals and channels. The shoals and channels act as dams and weirs, distorting the tides until they approximate those found in typical river estuaries. The tidal distortion results in a time asymmetry of the maximum currents which in turn produces a net up-harbor transport of sediments, despite the fact that the ebb currents are of the greater velocity. The hydrography of the harbor in spring, summer, and fall is described. Parameters discussed include salinity, temperature, transparency, water masses, tidal currents, sediment analyses, the salinity relations of intertidal flats, and some aspects of the annual temperature regime.

INTRODUCTION

Barnstable Harbor is located on the north shore of Cape Cod in Massachusetts. The harbor consists of an indentation of the original post-glacial coastline which has been nearly cut off by an offshore barrier bar. This type of origin is common to many of the tidal embayments of the East Coast. Their similarity in origin has endowed these embayments with certain "family" characteristics, and knowledge of one becomes (in varying degree) knowledge of all.

Among the "family" characteristics of this type of tidal embayment may be listed: low runoff which is carried by a few small streams and which, with direct rainfall and ground-water seepage, provides a total freshwater acquisition that is small compared to the quantity of tidal salt water entering and leaving the embayment; internal aquatic environments are essentially marine in character; and salt marshes drained by tidal creek systems border the open water. Barnstable Harbor exhibits these family characteristics.

[1] Contribution No. 995 from the Woods Hole Oceanographic Institution.

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PHYSIOGRAPHY

The harbor lies in an area of glacial till on the north side of the Sandwich Moraine left by the Wisconsin glaciation. The soil of the upland is primarily sand and sandy loam with scattered glacial boulders. The glacial till varies in depth from five to more than thirty feet and overlies disturbed glaciofluvial sand and gravel. In the region of the harbor the sandy till is separated from the disturbed sand and gravel by a layer of hard-packed grey till locally called "hardpan." Johnson (1925) and Mather *et al.* (1942) review the geology of the area.

The harbor is bordered on the southwest,

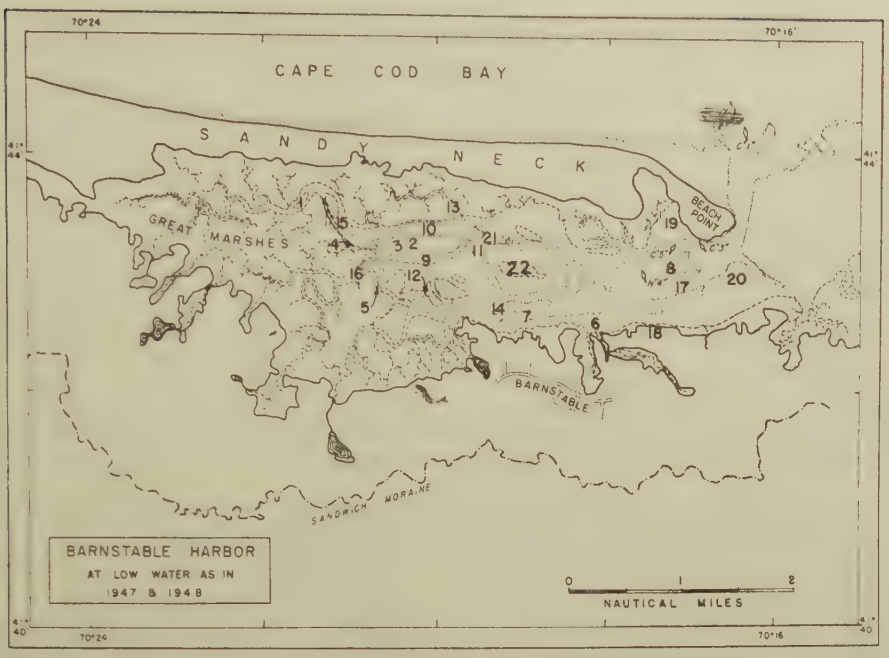

FIG. 1. Barnstable Harbor at low water as in 1947 and 1948. Dotted lines represent the junction of intertidal flats with open water; dashed lines represent the seaward edges of the salt-marsh; and a bold line indicates the meeting of salt-marsh and upland. The numbers refer to features named in Table 4.

west, and northwest by a salt marsh of considerably greater area than the harbor itself. Five major tidal creeks drain the marsh. Each tidal creek branches elaborately, and the main channels extend to the outer edge of the marsh where they receive small freshwater streams. Thirteen streams in total descend from the Sandwich Moraine and contribute to the harbor during each ebb tide about 0.3 million cubic feet of freshwater from a 22.8 square-mile watershed (Ayers 1956, p. 33).

On the north the harbor is bordered by a range of sand dunes which constitutes the barrier bar and is called Sandy Neck; this terminates in a broad sand spit at Beach Point (Fig. 1). Most of the dunes in this range are shifting, except in scattered areas where pitch pine, scrub oak, and dune grass have stabilized the sand. A continuous ocean beach lies along the north side of Sandy Neck.

Most of the harbor's inlet is occupied by intertidal sand flats. A channel cuts through these flats, but it widens and shoals offshore and terminates in a typical harbor bar at a depth of about five feet at mean low water.

At low water, shoals inside the inlet are exposed and reduce the navigable area to narrow channels. Early in the flood tide these shoals become submerged and allow water to enter through a much larger cross-section. The shoals produce a distortion of the tide which is discussed later as the "weir effect."

Numerous bars and shoals, extensive intertidal flats, and salt-grass covered islands standing two to five feet above the flats are the primary physiographic features within the harbor. In the inner parts of the harbor the intertidal flats rise about a foot above low water level. Flats rising two feet or more above the average level (three feet above low water) support the salt-grass *Spartina alterniflora* and are low (new) grassy islands.

The well-established marsh at the head of the harbor often presents cliff-like edges rising several feet above the level of the flats. Older portions of the marsh, farther back from the open water, appear to be about six inches higher than those adjacent to the harbor.

About 60 per cent of the total harbor

TABLE 1. *Mechanical analyses of surface soils from various parts of the harbor and marsh* Organic content determined as loss on ignition. Data of Harry J. Turner, Woods Hole Oceanographic Institution.

Location	% of sample passing through sieves of				Median diameter of particles, mm	Organic content, %
	20 mesh	48 mesh	100 mesh	200 mesh		
Channel-bar east of Wicks Is. (S)	98.3	80.3	18.5	0.6	0.20	3.2
WHOI flat (south side) (SM)	99.4	99.4	82.8	22.4	0.10	1.2
WHOI flat (center) (MS)	98.9	97.5	88.1	14.9	0.10	0.85
Howes' old flat (S)	99.8	97.8	77.8	6.3	0.12	0.60
Bung-hole flat (SM)	97.7	96.6	88.0	24.3	0.09	1.05
Gull Creek flat (SM)	98.7	94.1	69.4	20.0	0.12	1.3
Wicks Island (SS)	97.8	94.1	82.2	46.8	0.07	4.6
Marsh opposite Wicks Is. (SS)	98.2	96.5	85.2	35.1	0.09	3.0

20 mesh = 0.833 mm; 48 mesh = 0.295 mm; 100 mesh = 0.147 mm; 200 mesh = 0.074 mm; MS = muddy sand; SM = sandy mud; SS = sandy silt; S = sand.

bottom is exposed at low water. The western end of the harbor becomes almost completely exposed, the remaining water being confined to narrow channels which are extensions of the main tidal creeks.

The bottom is primarily fine muddy sand, though clean coarse sand occurs in the harbor mouth, and mud or sandy mud is dominant in the tidal creeks. Bottom samples from various parts of the harbor show a considerable variation in their contents of fine sediments (Table 1, column 5; see Table 4 and Fig. 1 for sampling locations). The greatest proportions of fines occur in the stabilized surface soils of the marshes and grassy islands. Moderate proportions are present in the surfaces of the somewhat less stable intertidal flats. Shifting flats of clean sand near the harbor mouth may be expected to contain the smallest proportions of fine sediments.

The harbor is shallow in all its parts above the mouth of Maraspin Creek (Table 4 and Fig. 1), and winds produce strong wave action. Local, usually temporary, silting-up and scouring occur in all parts of the harbor. Changes in the shallow inner end of the harbor consist chiefly of meanderings of the channels back and forth across the intertidal flats. There are indications (described below) that the head of the harbor, at least, is gradually filling in.

HYDROGRAPHY

The harbor ranges in depth from 8 to 30 feet at high water. The shallowness and the large tide range result in extreme volume changes during each tidal cycle The harbor volume changes from about 1000×10^6 cubic feet at high water to about 71×10^6 cubic feet at low water, the intertidal volume or tidal prism being about 93 per cent of the high-water volume. The large tidal exchange rather quickly carries to sea the small freshwater acquisition. About five tidal cycles are required to remove from the harbor a volume of freshwater equal to the quantity of freshwater accumulated in the harbor at a given high tide (Ayers 1956, pp. 32–33).

The Tides

The mean tide range at Beach Point is 9.5 feet; the range at spring tides is 11.0 feet (U. S. Coast & Geodetic Survey Tide Tables). Because shoals inside the harbor hamper the ebb current and produce an elevated low-water level, there is a reduction in tide range between the inlet and the head of the harbor. Neap tides do not inundate the salt marsh, while spring tides cover it to depths up to 1.5 feet.

As is common in small harbors along this coast, high and low waters occur at nearly the same time in all parts of the harbor, and maximum tidal currents occur near mid-tide. Preliminary tide-guage observations indicate, as first approximations, that the interval between high waters at Beach Point and the head of the harbor is about 0.5 hour, and that the interval between low waters at these points is about 0.9 hour.

TABLE 2. *Durations of ebb and flood tides in various parts of the harbor*
Head of the harbor begins with innermost weir.

Position	Date	Duration of flood, Hrs.-Min.	Duration of ebb, Hrs.-Min.	Remarks
Can 1	17–VI–48	6–15	6–15	Normal tidal cycle
				Major weirs at this level, 6 in. rise needed to stop ebb
Nun 4	27–X–47	5–45	5–45	
Main Channel at mouth of	21–X–47	6–25	6–15	
Maraspin Cr.	17–VI–48	5–45	7–0	
Yacht Club Channel	2–VI–48	5–45	6–35	Minor weir, 3 in. needed
	22–X–47	5–50	6–50	to stop ebb
			6–30	
	28–VIII–52	5–30	7–18	
Jct. North Channel with	8–VI–48	6–10	7–0	Minor weir, ca 3 in.
Phillis Is. Channel	17–VI–48	5–20	7–10	needed to stop ebb (estimated)
Midway, S of WHOI flat	22–X–47	5–45	7–0	
	20–X–47	5–5	6–40	
	17–IX–47	4–45	7–30	
		5–5		
	21–X–47	5–25	7–0	
			6–50	
Mouth of Scorton Cr.	2–VI–48	5–35	7–10	Net elevation of low water
	17–VI–48	5–40	7–25	level: ca 1 foot

Head of harbor average: Flood 5.5 hrs.; ebb 7.1 hrs.

The durations of flood and ebb in the upper harbor are about 5.5 and 7.1 hours, respectively (Table 2).

The weir effect

Shortening of flood and prolongation of ebb is typical of the tidal wave in shoal water (Doodson and Warburg 1941), but in Barnstable this effect is exaggerated by the shoals in the harbor.

At low water Horseshoe Shoal and the flats along shore beside it act as a dam with two weirs. The two weirs are narrow channels through which the tidal currents must pass during the hours when the shoal and adjacent flats are exposed. The pronounced reduction in cross-section at this point hinders and prolongs the outflow of the ebb tide and allows a head of water to develop above the weirs. The weirs retain this head until the waters outside the harbor have passed through their low water stage and begun their flood-tide rise.

The time used in overcoming the head of water above the weirs is the period during which the weakest flood current would flow into a harbor of more usual physiography. When the head is exceeded and the flood current begins to flow through the weirs, it soon reaches a velocity close to its maximum (Fig. 2).

Temporary tide staffs have shown that the tide outside the harbor rises about six inches before the ebb current ceases to flow out through the weirs at Horseshoe Shoal. This rise is sufficient to submerge a major part of Horseshoe Shoal and adjacent flats. The shoal and flats become completely submerged soon after the flood current begins to run in through the weirs.

Lesser weirs exist at Yacht Club Channel, where tide staffs have shown that the water rises about three inches before the ebb current stops. At the points where Midway and North Channel enter Phillis Island Channel, visual estimates suggest a further three-inch rise before the ebb ceases. The weirs result not only in distortion of the flood and ebb durations but also in an elevation of low water level along the length of the harbor (Table 2).

Figure 2 shows the surface current velocities observed during a tidal cycle in Yacht Club Channel and over the crest of an inter-

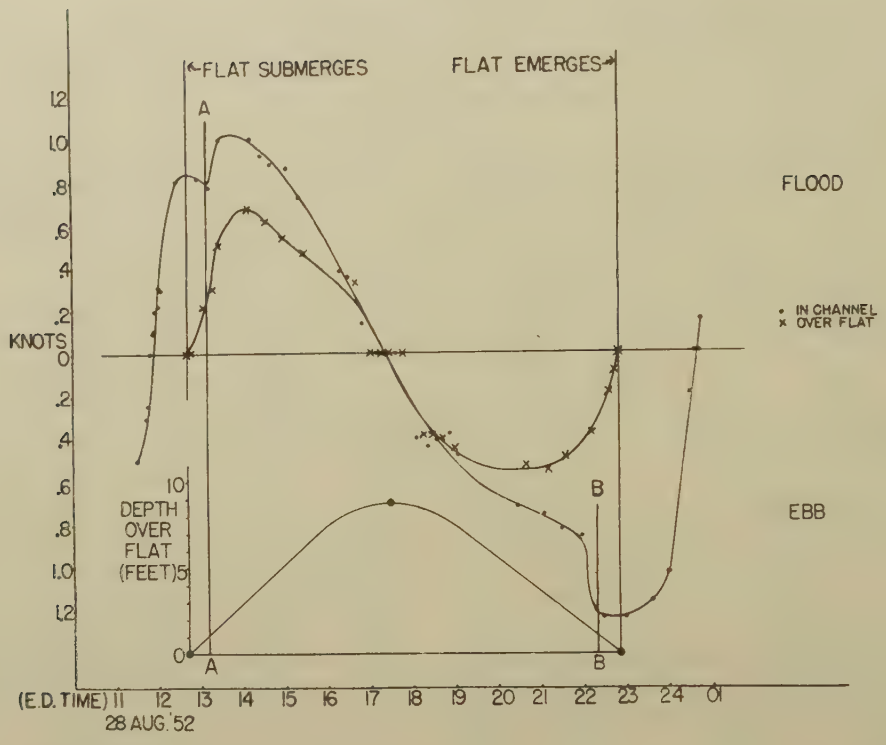

FIG. 2. Tidal current velocities in Yacht Club Channel and over the intertidal flat immediately north of that channel. 28 August 1952.

tidal flat immediately north of that channel. The very rapid increase of current velocity in the channel during early flood was interrupted by a plateau in velocity, beginning just before the adjacent flats became submerged and ending when the flats were about a foot under water (line AA). After the flats were overflowed the flood velocity in the channel quickly rose to its maximum of 1.03 knots, at the end of the second hour of flood, then declined steadily until the end of flood 3.5 hours later. The flood current over the flat attained its maximum velocity of 0.67 knot at the same time as did that in the channel and also went to zero at 5.5 hours of the flood tide, 4.7 hours after the flat's submergence.

During the first hour of ebb no velocity difference between the currents in the channel and over the flat was discernible. After 1.25 hours of ebb the current velocity over the flat became less than that in the channel. Ebb current over the flat attained its maximum velocity of 0.53 knot at the end of the third hour of ebb, after which it decreased steadily until the flat emerged after 5.5 hours of ebb. The current in the channel increased steadily to about 0.9 knot at 4.6 hours of the ebb when the water over the flat was about one foot deep (line BB); between that time and 5.1 hours of ebb (when there was about six inches of water over the flat) the channel current increased to 1.23 knots. It attained its maximum of 1.25 knots at 5.5 hours of the ebb when the flat emerged, then decreased to 1.03 knots at 6.6 hours, and went to zero at 7.3 hours of the ebb.

The data indicate that the ebb current experiences effective confinement to channels at a time when there is still about a foot of water over the flats. Prior to this time the freer drainage in the open channel tends to lower its water level and water from over the flat, retarded by friction with the flat, flows obliquely into the channel. The friction-

slowed water entering the channel requires acceleration from the channel current and causes a temporary decrease in the acceleration of the channel current (see Fig. 2 between 19 and 22 hours). By the time only a foot of water remains over the flat the quantity of friction-slowed water leaving the flat has become insignificant, and its retarding effect on the velocity of the channel current disappears (Fig. 2 between 22 and 23 hours).

A condition at least superficially similar to the above occurs during submergence of the flat on the flood tide. From just before the flat submerges until it is covered by about a foot of water the velocity of flood remains nearly constant. In this case the retarding effect of friction-slowed water that crosses the flat and the increasing cross-sectional area available as the flat becomes submerged both act to reduce current velocity in the channel. The flood velocity at this period is increasing, and the two retardant effects produce only a velocity plateau. The plateau disappears when the harbor's full cross-section becomes available for flow and when the quantity of water slowed by friction of the flat becomes insignificant in the total volume flowing (Fig. 2 between 12 and 14 hours).

Effects of tidal currents on bottom physiography

Maximum velocity of the flood current occurs near mid-flood when the intertidal flats are submerged and the cross-sectional area of the harbor is large. The flood current attains maximum surface velocities of 50 to 80 cm/sec. These correspond to average velocities of 37.5 to 60 cm/sec. (Sverdrup *et al.* 1942, p. 568) through the harbor's cross-section. These average velocities are ample (Sverdrup *et al.* 1942, Fig. 251) to erode sands of particle sizes 0.06 to 3.0 mm and to transport silt particles of 0.005 to 0.01 mm toward the head of the harbor. The flood current thus is capable of moving sediments up-harbor. Plankton nets towed at the times of maximum current capture large quantities of sediment.

Sediments carried up-harbor by the flood tide settle out at slack high water. Those settling into the channels are swept seaward during the ebb. Those sinking onto the flats are subjected, during the ebb, to currents less than those that brought them there (Fig. 2). The fact that the ebb currents over the flats are nearly zero when the ebb reaches its maximum in the channels indicates that some of the sediments dropped on the flats at slack high water are able to remain on the flats. That such is taking place is indicated by the formation of new (low) *Spartina*-covered islands on the intertidal flats, by local tradition that the upper harbor (at least) is shoaling, and by the fact that the flats contain more fine sediments than do the channels (compare row 1 with rows 2–6, Table 1). Once salt-grasses are established, mechanical trapping and plant decomposition products further increase the proportion of fines in the island and marsh soils.

Maximum ebb velocity in the harbor occurs after the intertidal flats are bared sufficiently to confine the current to the channels (Fig. 2). The maximum erosive effect of the ebb current is thus limited to the channels, which it keeps open. Apparently for this reason submerged bars protruding into the channels become recurved toward the harbor mouth. Also, this is probably the reason that the intertidal flats have their long axes lengthwise of the harbor. Horseshoe Shoal just inside the inlet apparently has a central portion that does not shift, though its arms point seaward as do the other flats of the harbor.

The effect of the asymmetry of the maximum currents on sediment transport is augmented by flotation. On calm days the flood tide overflowing the flats floats off many dry particles of sediment on the water's surface film. These particles are carried up-harbor until turbulence breaks the surface film and allows them to sink.

By these means the currents achieve a net movement of sediments toward the head of the harbor, even though the ebb current is stronger than the flood.

Water types

Two parent water types, and a mixture of the two, are present in the harbor and the

creeks tributary to it. They are: Cape Cod Bay Water, found at the mouth of the harbor; freshwater, entering at the periphery of the marsh; and Mixed Water, in the creeks and head of the harbor. Each type migrates back and forth under the influence of the tide.

At all stages of the tide, except in spring freshet conditions, Cape Cod Bay Water can be found along Beach Point below the weirs at Horseshoe Shoal. It is clear, greenish in color, and of salinity 31.50 to 32.50‰. The freshwater entering the creeks is typical swamp water. It is brown in color but free of silt. Its salinity near the limit of tidal influence ranges from 1.00 to 1.18‰.

The upper harbor and major portions of the tidal creeks are occupied at all stages of the tide by Mixed Water with characteristics between those of the main two types. This water is greenish-brown in color, is definitely turbid, and its salinity ranges from about 1.00‰ near the heads of the creeks to about 31.50‰ in the head of the harbor.

Tidal movements of water types

On the flood tide Cape Cod Bay Water moves into the harbor and by high water is found up-harbor to points beyond Sand

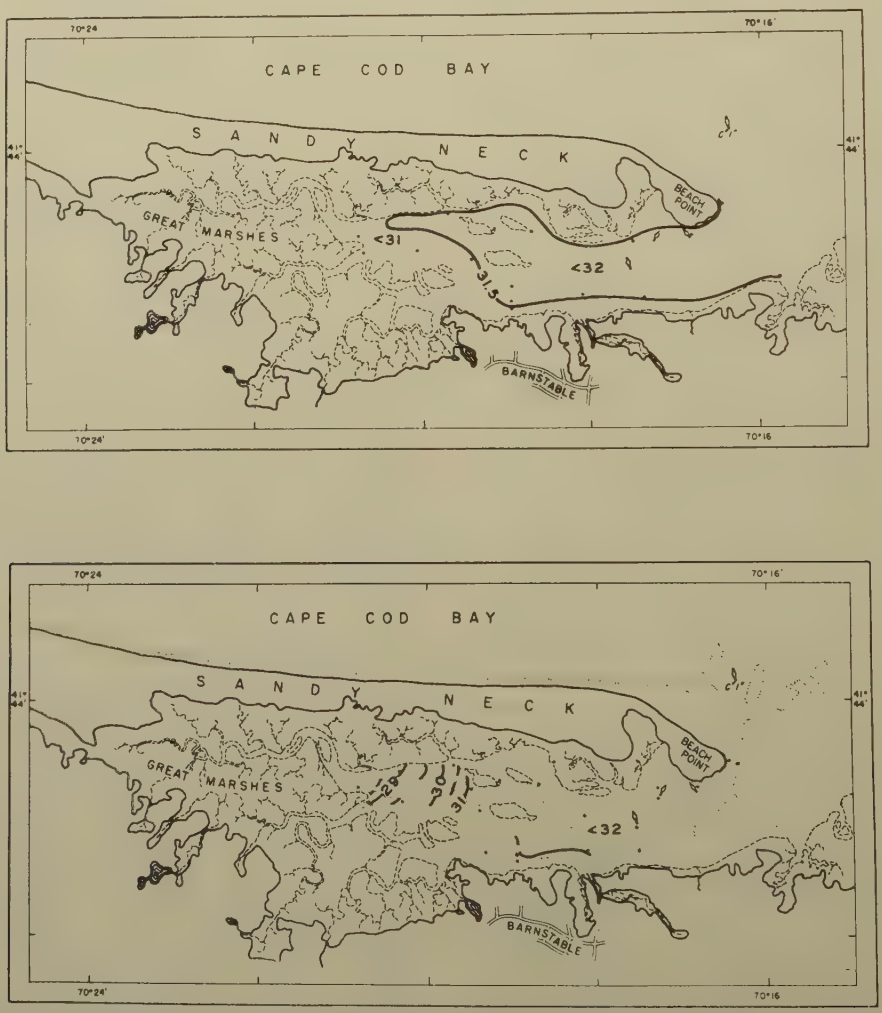

FIG. 3. Distribution of surface salinity (‰) in summer. 25 and 29 August 1947. *Above*: at high water. *Below*: at low water.

FIG. 4. Distribution of surface salinity (‰) in fall. 17 November 1947. *Above*: at high water. *Below*: at low water.

Island and Wells Creek. The advance and retreat of the tide cause extensive horizontal migration of the water and result in horizontal mixing. At full high water only a small amount of the Mixed Water remains in the upper harbor near the mouths of the creeks, while the tidal creeks are filled by it. By late ebb the column of high salinity water has retreated down the harbor, and the Mixed Water has followed it. At low tide, Cape Cod Bay Water is present only between the inlet and Horseshoe Shoal. During freshets it is forced out of the harbor. The horizontal distributions of salinity in summer and fall are shown in Figures 3 and 4. Figure 5 is the salinity distribution during spring freshet.

Above the mouth of Maraspin Creek very small vertical salinity gradients are occasionally found at high water and at low water. At other times no salinity gradient is present.

The salinity relations of intertidal flats

During the advance and retreat of the tide, water moving along the shores of the harbor is outrun by that in the middle of the channels. As a result, intertidal flats along the shores are subjected to less salinity

FIG. 5. Distribution of surface salinity (‰) during spring freshet. 12 and 16 April 1948. *Above*: at high water. *Below*: at low water.

TABLE 3. *Salinity ranges in various parts of Barnstable Harbor*
Spring freshet conditions are starred.

Location	Salinity range, ‰	Position in harbor
Beside WHOI flat	20.46*–31.40	Head of harbor
Off Sand Island	29.63 –31.73	Near head of harbor
Phillis Island Channel	24.51*–31.89	Near middle of harbor
Off Maraspin Creek mouth	27.38*–31.71	Below middle of harbor
Off Cobb's Village	28.49*–31.62	South shore near inlet
The Cove	28.62*–31.67	North shore near inlet
Beside Yarmouthport flat	31.38 –32.14	South shore, at inlet

TABLE 4. *Orientation table*
The numbers in Figure 1, and the station letters in the B and D parts of Figures 7 through 10, indicate the following locations.

1. Wicks Island
2. Experimental area of Woods Hole Oceanographic Institution
3. Howes' flat
4. Bung-hole flat
5. Gull Island flat
6. Maraspin Creek
7. Yacht Club Channel
8. Horseshoe Shoal
9. Midway Channel
10. North Channel
11. Phillis Island Channel
12. Sand Island
13. Wells Creek
14. Scudders Lane Landing
15. Scorton Creek
16. Spring Creek
17. Fisherman's Gut
18. Cobb's Village
19. The Cove
20. Yarmouthport flats
21. Big Thatcher Island
22. Phillis Island

A. Buoy "C 1"
B. Buoy "C 3"
C. Buoy "C 5"
D. Buoy "N 4"
E. Main channel, off Maraspin Creek
F. "14" in Figure 1
G. Main channel, west of Phillis Island
H. North Channel, off mouth of Wells Creek
I. "15" of Figure 1
J. Buoy "C 3"
K. "7" of Figure 1
L. Midway, south of the W. H. O. I. flat
M. "16" of Figure 1
N. North edge of Beach Point, west side of channel
O. "9" in Figure 1
P. North edge of Beach Point, east side of channel
Q. "11" in Figure 1
R. North Channel, north of W. H. O. I. flat
S. "17" in Figure 1

variation during a tidal cycle than are flats in the center of the harbor. Similar conditions have been observed in the Tees (Alexander *et al.* 1935) and in the Tamar (Milne 1938).

Although flats along the axis of the harbor are subject to more salinity variation than those along the shore, they are not subject to the whole salinity range of that part of the harbor. At low tide the least saline water encircles them, but does not cover them. It is pushed up-harbor before the flats are overflowed by the flood tide, and the flats have emerged before this water returns again during the late ebb. In the same fashion, tidal pools on the higher grassy islands are of greater salinity than those on lower islands. Increased evaporation during their longer periods out of water may also contribute to their increased salinity.

The distance of a flat from the mouth of the harbor determines which water types bathe it. Most of the flats are submerged only during the more saline two-thirds of the normal salinity range obtaining in that part of the harbor.

Table 3 gives the salinity ranges of the water in various parts of the harbor. All of the salinities observed have been used; they include conditions of drouth, of spring freshet, and of all stages of the tide. In those parts of Table 3 which include freshet values, the normal variation in salinity is approximately the most saline one-quarter of the range indicated.

Temperature distribution

Water temperatures in the harbor do not reflect the origin or composition of the water, for they depend upon the previous association of the water with the harbor. Water which has ascended furthest into the harbor is the warmest or coolest depending upon the season. In spring and summer, water passing up the harbor is warmed; in fall and winter it is cooled. The temperature of the water in any part of the harbor at low tide reflects (by its degree of heating or cooling relative to the Cape Cod Bay Water at Beach Point) the previous high-tide position of that water in the harbor.

Water remaining in the harbor at low tide is essentially isothermal from surface to bottom. The tortuous nature of the channels, irregularities on the channel bottoms, and the high velocity of the late ebb current produce thorough mixing.

During early flood the channels overflow; in spring and summer the overflowing water absorbs heat which the flats have

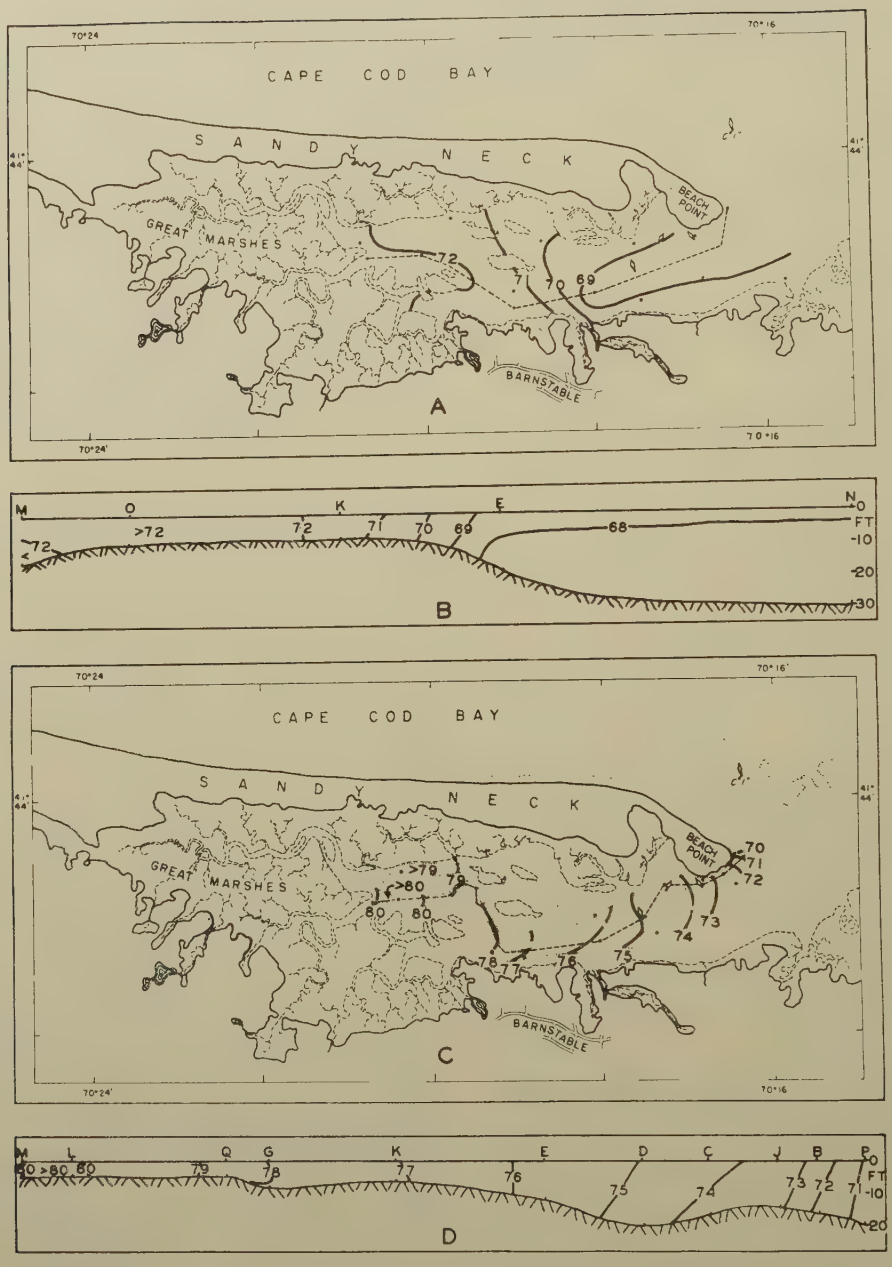

FIG. 6. Horizontal and vertical distributions of temperature (°F) in summer. 25 and 29 August 1947. Heavy dashed lines in A and C show the positions of vertical sections B and D. Station letters in B and D are as listed in Table 4. A and B at high water; C and D at low water.

acquired during their exposure to the sun and air. After the flats become submerged, the water is still shallow enough for sunlight to reach bottom throughout most of the flood tide period. During this time continued warming of the bottom by the sun and continued transfer of heat from bottom to water are both probable.

A similar warming occurs during ebb when water over the flats becomes shallow and

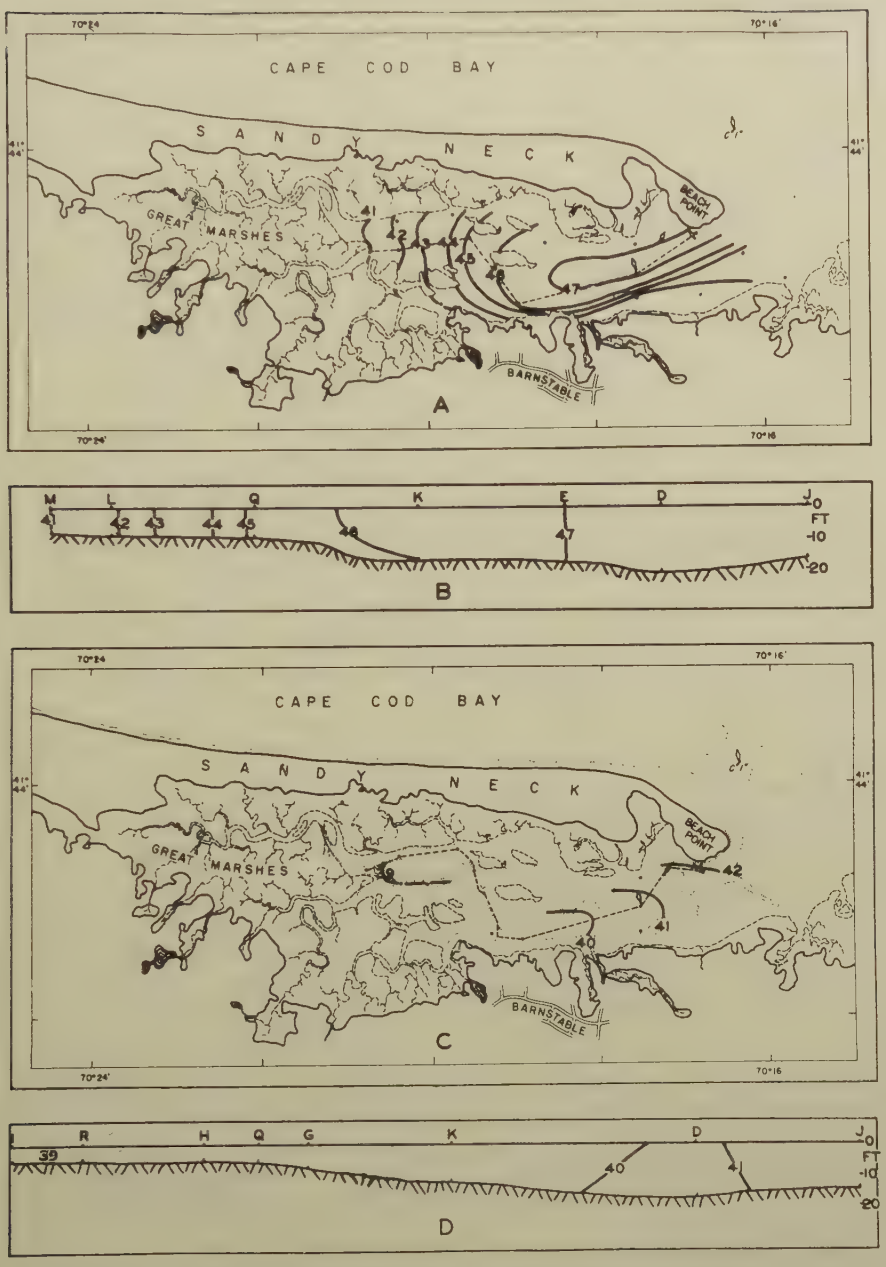

FIG. 7. Horizontal and vertical distributions of temperature (°F) in fall. 17 November 1947. Heavy dashed lines in A and C indicate the positions of vertical sections B and D. Station letters in B and D are listed in Table 4. A and B at high water; C and D at low water.

recedes from the flats. The warming taking place during the ebb tide is more readily noted than that during the flood, for by low tide the warmed waters have accumulated in the channels.

In surveys made at high water during the spring and summer the subsurface water is occasionally observed to be warmer than the surface. This water appears to be unstable and the condition temporary. In

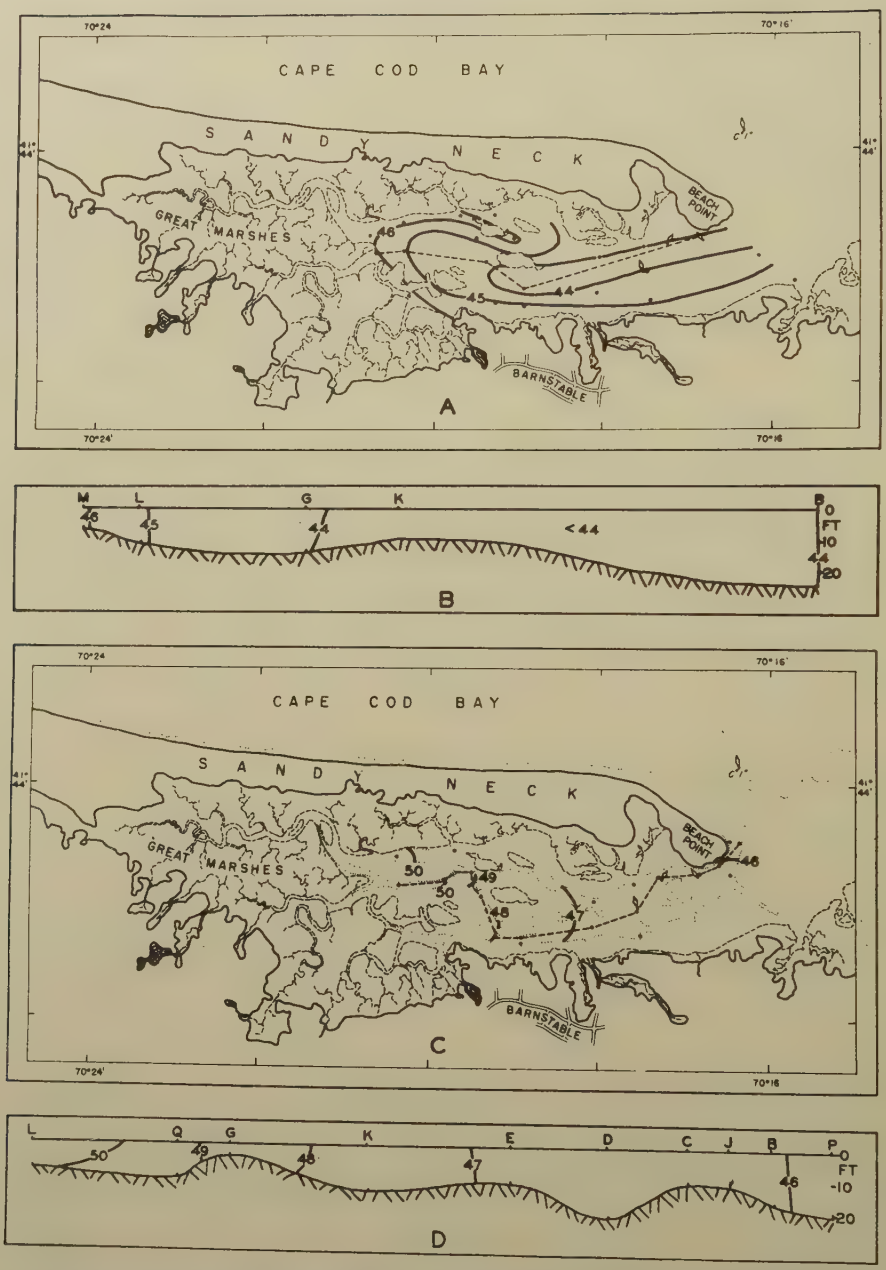

FIG. 8. Horizontal and vertical distributions of temperature (°F) during spring freshet. 12 and 16 April 1948. Heavy dashed lines in A and C indicate the positions of the vertical sections B and D. Station letters in B and D are listed in Table 4. A and B at high water; C and D at low water.

practically all cases this occurs in water shallow enough for sunlight to penetrate to bottom.

Figures 6, 7, and 8 show temperature distributions in summer, fall, and spring.

The transition periods

Twice a year the harbor goes through a transition period when its temperature approaches that of Cape Cod Bay. One of these periods occurs in late March or early

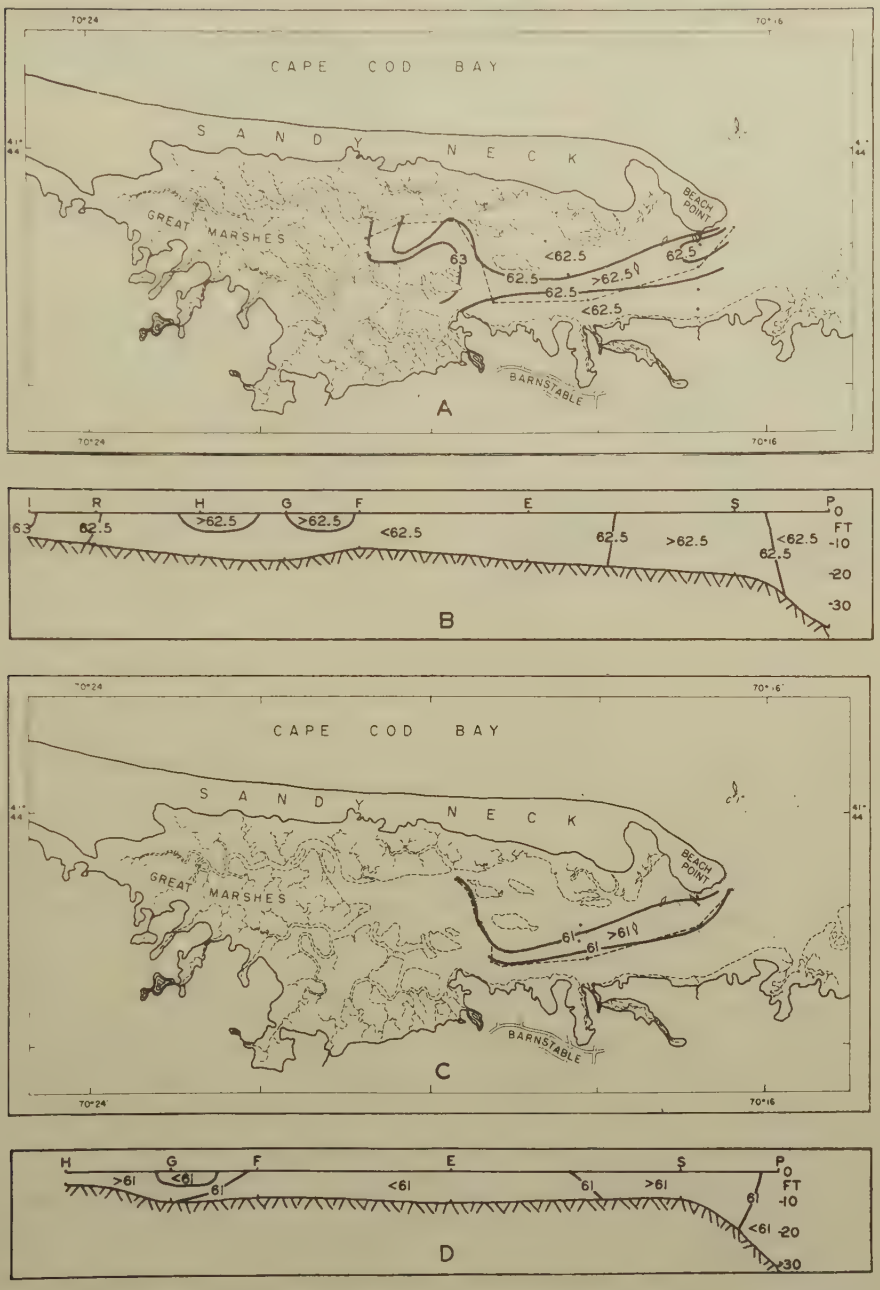

FIG. 9. Horizontal and vertical distributions of temperature (°F) during the fall transition period. 23 September 1948. Heavy dashed lines in A and C show the positions of the vertical sections. Station letters in B and D are listed in Table 4. A and B at high water; C and D at low water.

April when the harbor's rather rapid spring warming overtakes the slower warming of Cape Cod Bay. The other occurs when the harbor's rather rapid autumn cooling overtakes the slower cooling of Cape Cod Bay. At these times high-water and low-water temperatures become very nearly alike. In 1948 the fall transition took place during

the latter part of September; Figure 9 presents surveys made on September 23rd.

Transparency

In summer, light penetrates to different depths in various parts of the harbor. Transparencies by white Secchi disc range from 6.5 feet in the Mixed Water at the head of the harbor to more than 13 feet in the Cape Cod Bay Water at Beach Point.

The decrease in transparency toward the head of the harbor is a reflection of the increasing amounts of plankton and suspended sediments which occur there.

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Thermal Changes Accompanying the Compression of Aqueous Solutions to Deep-Sea Conditions[1]

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ABSTRACT

Apparatus is described for studying the effects of high hydrostatic pressure on the viability, reproduction, and physiological reaction rates of bacteria in aqueous solutions. Rapidly compressing such solutions to deep-sea conditions results in temperature increases ranging from 2 to 5°C. Decompressing the system to ambient pressure results in cooling to a corresponding degree. When the apparatus is submerged in constant temperature water bath, the thermal time constant T-63 of solutions compressed or decompressed in the steel pressure vessel is generally less than 3 minutes. The degree of heating or cooling is primarily a function of the change in hydrostatic pressure and the ambient temperature. To a lesser extent heating or cooling is influenced by the chemical composition of the solution. The degree and duration of thermal changes may be minimized by the use of small pressure vessels submerged in constant temperature bath and by slow compression or decompression. Thermal changes were measured by bead-type thermistors, which must be calibrated for use at each pressure and ambient temperature.

INTRODUCTION

Hydrostatic pressures of a few hundred atmospheres influence the multiplication, viability, and metabolic activities of bacteria and allied microorganisms (ZoBell and Johnson 1949, ZoBell and Oppenheimer 1950, and Kitching 1957). Such effects may be appreciable in the sea where pressure approaches 1100 atmospheres in the greatest known deeps (Wüst 1951, Carruthers and Lawford 1952). Some of the effects of deep-sea pressures on apparatus have been described by ZoBell (1954). Hydrostatic pressure in the sea increases with depth by approximately 0.1 atm/m, the pressure-depth gradient being influenced only slightly by latitude, salinity, or by temperature (Bjerknes and Sandström 1910). One atmosphere is equivalent to 14.696 lb/in^2 (psi), 1.0332 kg/cm^2, 1.0133 bars, or to 760 mm Hg at 0°C.

Since biochemical reaction rates are extremely sensitive to temperature changes, and since the biological effects of pressure are influenced by temperature, it is of utmost importance that the temperature of experimental material be controlled and known. Near the threshold of pressure-temperature tolerance of a biological system, temperature changes resulting from changing pressure may be critical. Controlling the temperature during the compression or decompression of experimental material is complicated by adiabatic heating or cooling. According to Ekman's computations (Sverdrup *et al.* 1942), the heat of compression in the sea ranges from 0.016 to 0.209°C per 100 atm, depending upon the salinity, temperature, and depth of the water. The heat of compression is the heat which flows out of the liquid as it is compressed isothermally.

The heat of compression of complex experimental apparatus employed for investigating the effects of hydrostatic pressure on biological systems cannot be computed from theoretical consideration owing to the anomalous behavior of the heterogeneous components (steel, glass, water, solutes, etc.). If applied adiabatically, the heat of compressing the average biological liquid to 1000 atm would be sufficient to raise its temperature several degrees, the exact rise being a

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function of the ambient temperature and the composition of the liquid. In actual practice the temperature change during the compression of experimental material is less than adiabatic, because of the thermal behavior of the vessel itself and the dissipation of heat to the surroundings. As pointed out by Dorsey (1940), it is extremely difficult to obtain accurate dynamic or experimentally observed values on the thermal properties of water at different pressures owing to the effects of the enclosing and measuring apparatus. The calculation of static or theoretical values for the heat of compression of water is complicated by the concurrent effects of compression on volume, specific heat, conductivity, and molecular species. Tammann and Elbrächter (1931) were unable to explain differences between the static (computed) and dynamic (observed) values on the decrease of water temperature on adiabatic expansion. The compressibility of water is a function of temperature, its relative volume when compressed to 1000 kg/cm^2 being 0.9567 at 0°C, 0.9741 at 50°C, and 0.9984 at 95°C as compared to a volume of 1.000 under standard conditions (Bridgman 1931).

Therefore, efforts have been made to measure temperature changes which result from pressure changes in experimental materials rather than to measure the heat of isothermal compression. The steel pressure vessels, described below, were kept in a constant temperature water bath during compression and decompression in order to dissipate heat as rapidly as possible as in routine experimental operations. The temperature of aqueous solutions in vessels was recorded continuously at pressures up to 1000 atm and at ambient temperatures ranging from 5 to 55°C. The setup and manipulations in all details simulated the conditions employed in studying the effects of pressure on biological systems.

DESCRIPTION OF APPARATUS

Although designed primarily to study the effects of deep-sea pressures on the viability, reproduction, and biochemical reaction rates of microorganisms, the apparatus has also proved to be useful for investigating the pressure tolerance of lenses, light globes, electromagnets, insulating materials, and other apparatus. The pressure vessel (Fig. 1) is constructed of 18-8 type 303 stainless steel. Such steel has been selected as the best practical compromise among the requisite properties, including relatively high tensile strength with some elasticity, machinability, and chemical inertness or resistance to corrosion.

A vessel having an inside diameter of 1⅜ in. and 11 in. long holds 25 10 x 25-mm stoppered culture tubes and weighs less than 15 lb. Pressure vessels of greater capacity have been fabricated from steel cylinders of greater length or of greater diameter, but the larger ones are rather unwieldy and heat of compression is dissipated more slowly. When the internal diameter of the pressure vessel is increased, it is necessary to increase the wall thickness or external diameter according to the formula of Lamé (Laurson and Cox 1954):

$$S = P \frac{R^2 + r^2}{R^2 - r^2}$$

where S is the tensile strength of the structural material, P is the internal pressure, R is the outer radius, and r is the inner radius. Hamann (1957) expresses the yield pressure of thin walled cylinders simply as $P = (K-1)S$, where K is the ratio of outer to inner radius. We have in use a hundred vessels like the one illustrated in Figure 1, which have been tested at pressures up to 2000 atm.

When properly fitted with an O-ring, the cap can be screwed on by hand to give a pressure-tight seal without the use of a wrench. It may be necessary to use a Stilson or strap wrench, however, to remove the cap after the vessel has been subjected to high pressure owing to the extrusion of the O-ring into the crack between the cap and vessel top. The smooth machine finish at the top of the vessel and the groove which accommodates the 7/64-in. O-ring must be machined with a precision of ±0.005 in. Otherwise minute valleys may permit the O-ring to be extruded all the way through with a resultant loss of hydraulic fluid and

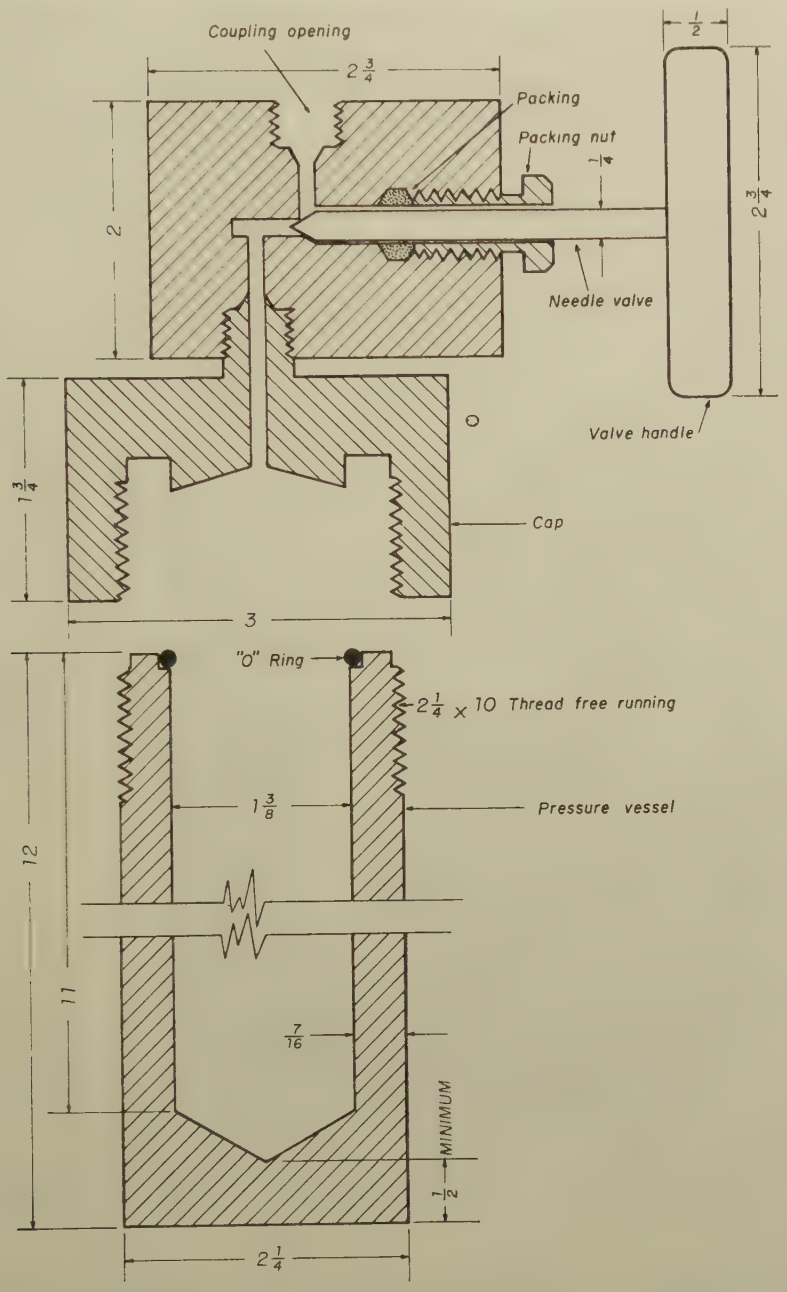

FIG. 1. Cross section of pressure vessel showing cap and needle valve.

pressure. Similarly, a particle of grit, sand, broken glass, or other solid object may keep the cap from coming sufficiently close to the top of the vessel with resultant failure at high pressure. With ordinary precautions, however, such failures are rare. In thousands of cases it has been our experience that when a properly closed vessel holds high pressure initially, constant pressure is maintained thereafter almost indefinitely, provided the temperature is kept constant.

O-rings of various sizes and compositions

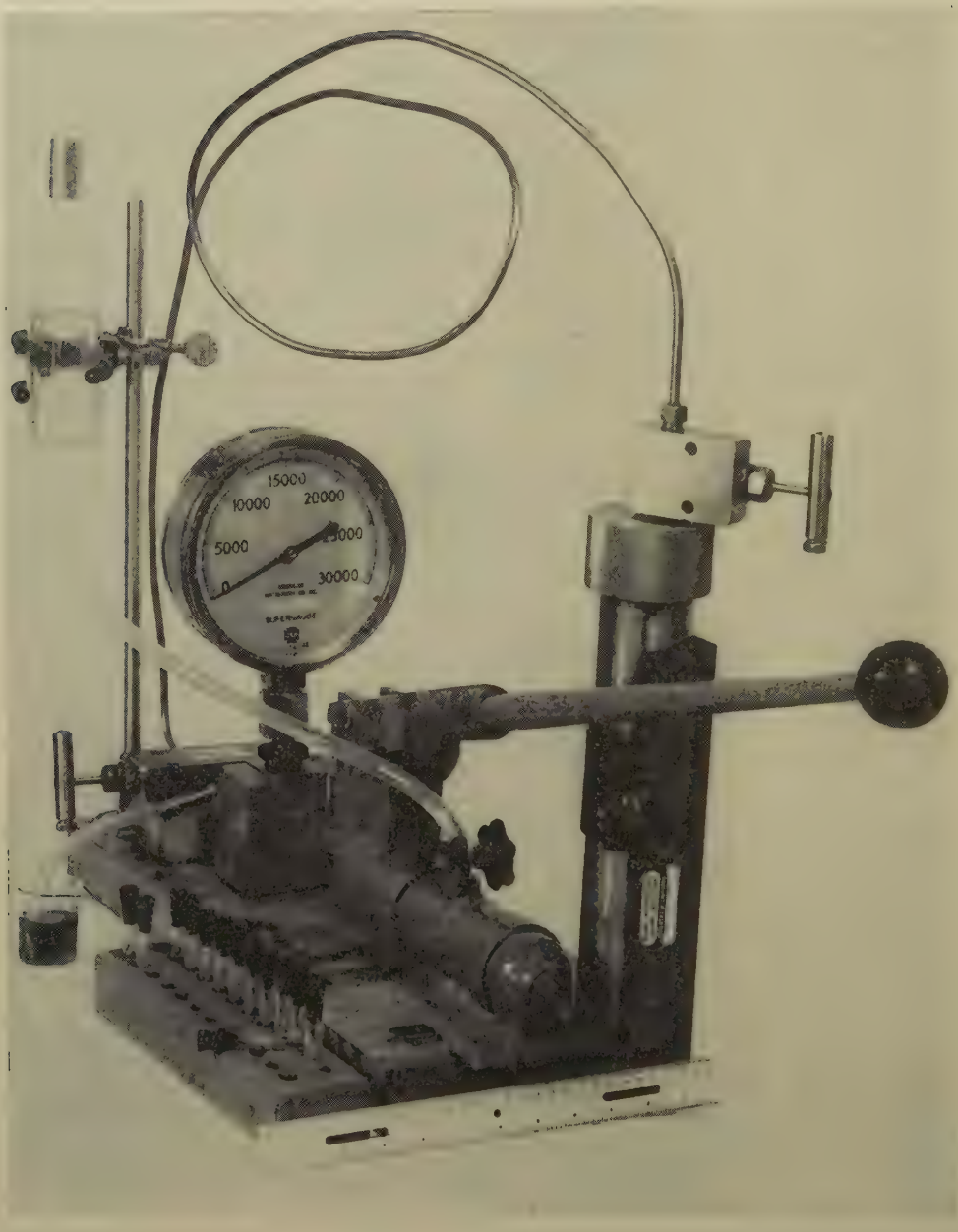

FIG. 2. Assembled pressure vessel connected to hydraulic pump and connecting gauge. Hydraulic fluid flows by gravity from the transparent reservoir into the pump. Beside the assembly is a rack for 10 x 50 mm culture tubes.

are obtainable from Parker Appliance Co., Cleveland, Ohio. The 165-degree funnel-shaped ceiling in the center of the cap is for the dual purpose of securing the O-ring and of expelling gas from the vessel. It is so designed that when the vessel is filled to the rim with hydraulic fluid, the fluid will be forced through the opening in the cap and to the top of the coupling opening in the needle valve without overflowing when the cap is screwed firmly in place.

The threaded male extension at the top of

the cap accommodates a stainless steel superpressure needle valve of the type manufactured by American Instrument Co., Silver Springs, Maryland. Each cap is fitted with a valve. The 59-degree conical tip at the top of the cap fits a corresponding 60-degree female conical seat in the valve, which when seated with a wrench gives a pressure-tight joint. The same union-type joint is employed to connect the assembled pressure vessel to the hydraulic pump (Fig. 2) with an appropriate length of stainless steel pressure tubing (o.d. $\frac{1}{4}$ in. x i.d. $\frac{3}{32}$ in.).

Figure 2 shows the complete apparatus, including a rack of 10 x 25-mm stoppered culture tubes of the type that are placed inside the vessel. This portable apparatus can be clamped to a work bench in the field, aboard a ship, or in the laboratory.

In the following experiments, designed to determine the heat of compression of biological materials under different conditions, the pressure vessel was kept completely submerged in a constant temperature water bath. It was secured in the vertical clamp, as pictured in Figure 2, only for the purpose of connecting it to the tubing and pump.

Pressures up to 1000 atm (about 15,000 psi), such as occur at a water depth of 10,000 meters, were applied to the vessel in about 30 seconds by several strokes with the pump handle. Hydraulic pumps distributed by American Instrument Co. or by Fred S. Carver, Inc., Summit, New Jersey, have given satisfactory service. Our preference, though, is for large capacity (30-ton) truck jack pumps manufactured by Blackhawk Mfg. Co., Milwaukee 46, Wisconsin. Shown in Figure 2 is a modified truck jack pump connected with a pressure gauge, a system of bleeder valves, and a reservoir of hydraulic fluid. A 1:1 mixture of glycerol and water makes a satisfactory hydraulic fluid. Glycerol is easier to remove from experimental material than oils commonly recommended for use in high pressure pumps. Moreover, the diluted glycerol is less likely to attack rubber packings.

The temperature on the inside of the pressure vessel was measured with a Western Electric Co. 14-B bead-type thermistor. The thermistor (Becker *et al.* 1947) is a glass-enclosed, semiconducting bead of metallic oxides whose resistance is a function of the ambient temperature. It was connected with special insulated leads through the cap of a pressure vessel (Fig. 3) to a Wheatstone bridge and a Leeds & Northrup type-G Speedomax recorder, calibrated to record the temperature continuously. In later work a Varian model G-11 strip chart recorder gave equally good results. Calibration values at specified temperatures from 5 to 55°C and at pressures up to 1000 atm were found to be constant and reproducible with an accuracy of 0.02°C.

CALIBRATION OF THERMISTORS

The resistance of each thermistor tested was found to be almost but not exactly a linear function of ambient temperature. The resistance (and consequently the thermometric behavior) of the thermistors is also influenced by pressure. It was necessary, therefore, to calibrate each thermistor for the temperature and pressure at which it was to be employed. First, it was calibrated at the ambient temperature at which it was to be employed at atmospheric pressure. This was done by adjusting the Wheatstone bridge resistances to provide for temperatures being recorded directly and correctly 5°C below to 5°C above each ambient temperature at which measurements were made. Within any 10° range between 0° and 60°C, the resistance of the 14-B thermistors was found to be directly proportional to temperature to the nearest 0.02°C.

At constant temperature (which is very difficult to realize experimentally at increasing pressures) the resistance of bead-type thermistors is influenced by hydrostatic pressure. This is illustrated by data from a representative run recorded in Table 1; compressing the system to 1000 atm starting at an ambient temperature of 25°C resulted in the thermistor's registering an apparent temperature of 28.81°C. Part of this increase was from heat of compression, but part is a reflection of the effect of pressure on the resistance of the thermistor, because when equilibrium conditions were established after half an hour by the dissipation of heat of compression in the water bath at 25°C, the

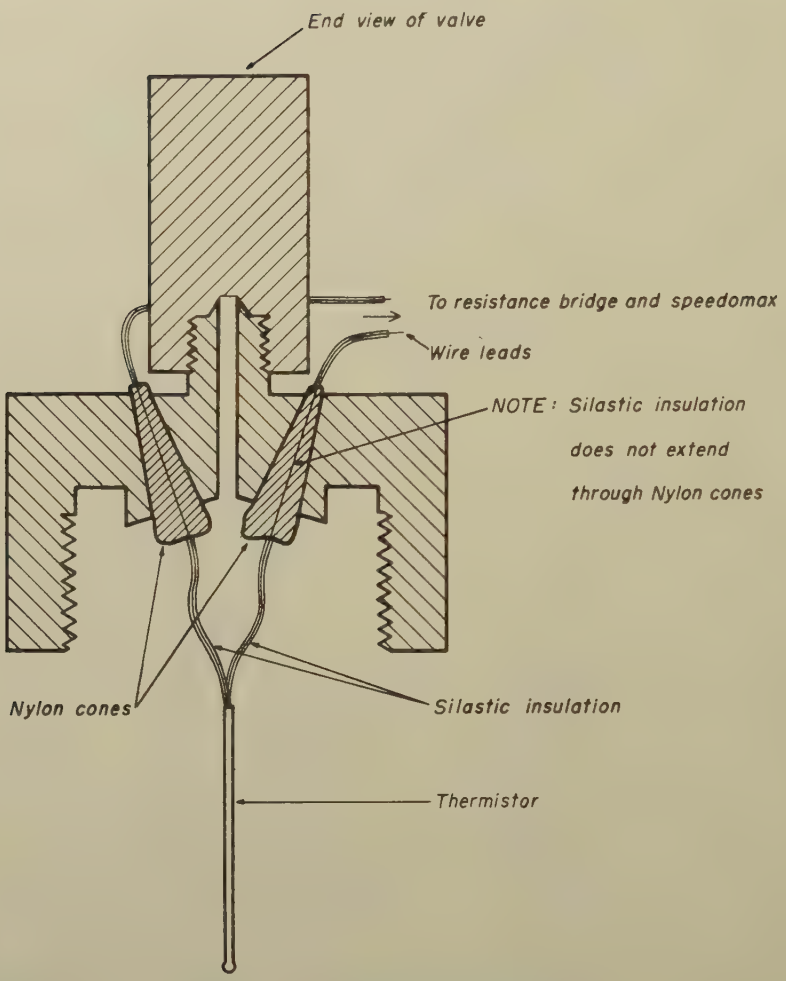

FIG. 3. Pressure vessel cap fitted with a thermistor. The current-conducting wires are insulated with a thick layer of Dow-Corning Co. "silastic." Nylon cones provide both insulation and a pressure-tight seal for the holes through which the wires pass.

thermistor registered 25.81°. In this case, the 0.81 increment represents the effect of pressure on the resistance of the thermistor. This is substantiated by the decompression of the system (see columns 7, 8, and 9 in Table 1). Immediately following decompression of the system to atmospheric pressure, it was cooled to an apparent (and actual) temperature of 21.99°C, or 3.01°C below ambient water bath temperature. Within half an hour the system was warmed by absorption of heat from the water bath until it reached equilibrium at 25.00°C. Repeating the operations any number of times yielded identical results within the limits of accuracy of the thermistor and the constancy of the water bath. When operating at 25 to 55°C, the water bath temperature remained constant to ± 0.02°, but it fluctuated by as much as 0.05° at 5°C.

The effect of compression on the resistance of thermistors in terms of °C is the compression correction factor which must be substracted from the apparent temperature registered by the thermistor at increased hydrostatic pressure to give the actual temperature. Table 2 shows these factors at ambient temperaturs ranging from 5 to 55°C at pressures from 100 to 1000 atm. For the 14-B bead-type thermistors, these

TABLE 1. *Apparent and corrected or actual temperatures recorded by 14-B bead-type thermistor in water-filled pressure vessel upon compression to 1000 atm for two hours followed by decompression in constant temperature bath at 25°C*

Time in minutes	Pressure in atm	Thermistor readings	Apparent Δt in °C	Corrected Δt in °C	Time in minutes	Pressure in atm	Thermistor readings	Corrected Δt in °C
0	1	25.00	0.00	0.00	120	1000	25.81	0.00
1	1000	28.81	3.81	3.00	121	1	21.99	3.01
2	1000	27.89	2.89	2.03	122	1	22.89	2.11
3	1000	27.40	2.40	1.59	123	1	23.45	1.55
4	1000	27.18	2.18	1.37	124	1	23.63	1.37
6	1000	26.81	1.81	1.01	126	1	23.97	1.03
8	1000	26.55	1.55	0.74	128	1	24.26	0.74
10	1000	26.35	1.35	0.54	130	1	24.45	0.55
15	1000	26.07	1.07	0.26	135	1	24.74	0.26
20	1000	25.93	0.93	0.12	140	1	24.88	0.12
25	1000	25.85	0.85	0.04	145	1	24.96	0.04
30	1000	25.81	0.81	0.00	150	1	25.00	0.00
60	1000	25.81	0.81	0.00	160	1	25.00	0.00
120	1000	25.81	0.81	0.00	240	1	25.00	0.00

In this series the compression correction factor is 0.81.

TABLE 2. *Compression correction factors for 14-B bead-type thermistor at different ambient temperatures and pressures*

Pressure in atm	Ambient temperature ± 0.05°C						
	5°	15°	25°	35°	45°	55°	Average
100	0.09	0.08	0.08	0.10	0.09	0.10	0.09
200	0.17	0.18	0.20	0.19	0.19	0.19	0.19
300	0.29	0.30	0.31	0.32	0.31	0.32	0.31
400	0.39	0.42	0.40	0.39	0.40	0.40	0.40
500	0.50	0.50	0.48	0.49	0.51	0.48	0.49
600	0.56	0.57	0.58	0.60	0.59	0.59	0.58
800	0.69	0.70	0.75	0.75	0.73	0.78	0.73
1000	0.86	0.85	0.83	0.86	0.88	0.91	0.86

factors approximate 0.1°C per 100 atm. This is somewhat more than the compression correction factors which Tavernier and Prache (1952) found for flat disc-type thermistors. Although the correction factors vary slightly with each thermistor unit, the factor appears to be independent of ambient temperature within the range of 5 to 55°C.

Owing to thermal and electrical conductivity changes induced in the element, the thermal time constant of 14-B thermistors in water was found to range from 20 to 30 seconds at 1000 atm as compared with approximately 1 second at 1 atm. The "thermal time constant" is the time required for the temperature of the element after being heated to change 63% of the difference between its initial temperature and that of its surroundings.

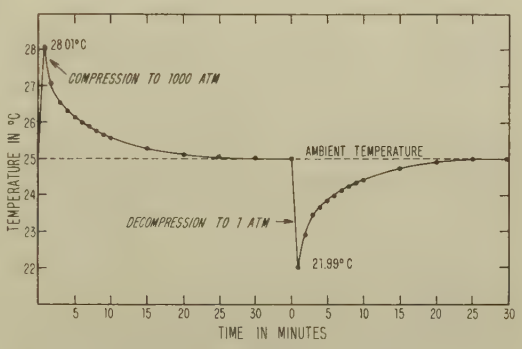

FIG. 4. Temperature changes occuring in gas-free water in steel vessel in constant temperature bath at 25°C when (1) compressed to 1000 atm within one minute, (2) held at 1000 atm for 30 minutes, (3) decompressed, and (4) held at atmospheric pressure for 30 minutes.

EXPERIMENTAL RESULTS

Filled to capacity with water, nutrient medium mineral salts solutions, or other aqueous biological materials, the closed pressure vessel, fitted with a calibrated thermistor, was submerged in a 60-gallon water bath at stated constant temperature. With the application of pressure there was an instantaneous increase in temperature (Fig. 4), from 30 to 60 seconds being required to compress the system to 1000 atm and to close the check valves. The temperature then commenced to fall as the heat of compression was dissipated in the water bath. Within 20 to

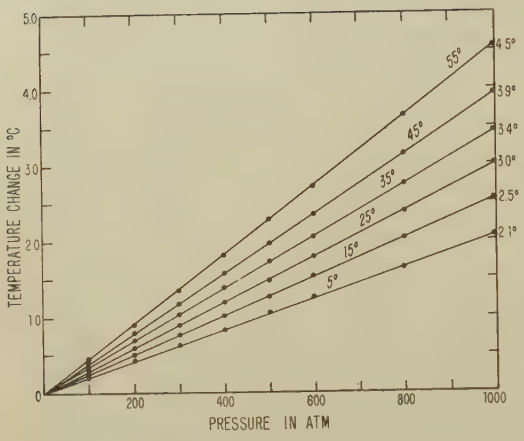

FIG. 5. Maximum temperature changes resulting from compression of gas-free water in steel vessels at ambient temperatures ranging from 5 to 55°C.

30 minutes, depending upon the pressure and consequent warming, the temperature of the compressed system returned to ambient. When equilibrium was established, the valves were opened permitting the pressure of the system to return to atmospheric. This resulted in instantaneous cooling (Fig. 4), after which another 20 to 30 minutes was required for the system to warm back to ambient.

Although not an actual measure of adiabatic heating or cooling, the procedures outlined above give a good approximation of the temperature changes which occur during the compression and decompression of experimental materials. Figure 5 shows the magnitude of the changes in gas-free water at ambient temperatures between 5 and 55°C at pressures up to 1000 atm. Within these extremes and the limits of experimental error, excluding anomalies in the behavior of heterologous systems, heat of compression increases with ambient temperature as almost a linear function of pressure.

At concentrations ordinarily found in aqueous biological materials (nutrient media, physiological salt solutions, etc.), dissolved substances have relatively little influence on the heat of compression. Higher concentrations of solutes, however, affect the heat of compression to the extent that the solutes affect compressibility and thermogenic reactions of system components. Among the many properties of liquids and solids affected by pressure are chemical reactivity, solubility, thermal conductivity, specific heat, and volume. Gases are responsible for pronounced effects of pressure; in the foregoing experiments gases were carefully excluded. The heat of compression of a 50 per cent solution of glycerol in water, employed as hydraulic fluid in the experiments, has approximately double the heat of compression of pure water. Thus the introduction of this hydraulic fluid into the pressure vessel results in anomalously high heat of compression values. Other small anomalies result from friction between the glass envelope and metallic oxides encased in the thermistor, unequal expansion or contraction in parts of the steel pressure vessel, and other mechanical effects of pressure on heterologous components, including glass culture tubes, rubber stoppers, etc.

More important than the chemical composition of the aqueous system in determining maximum heating during compression of experimental materials is the rate of compression or decompression. This will be apparent from the cooling and heating curves in Figure 4. In such experiments maximum heating occurs when pressure is applied rapidly, allowing little time for heat to be dissipated in the vessel itself and in the water bath. Gradually increasing the pressure to 1000 atm during a period of 30 minutes rather than in 30 seconds, for example, results in only negligible temperature changes. Applying pressure at the rate of heat dissipation is not always a practical means of controlling the temperature, however, because in certain experiments the biologist is concerned with reaction rates during the first few minutes of compression. In experiments such as those of Johnson (1948) on the effects of pressure on bioluminescence reaction rates or those of Johnson and ZoBell (1949) on the effects of pressure on the thermal disinfection of spores, for example, small (diameter $9/16$ in.) pressure vessels were employed to provide for the rapid dissipation of heat of compression.

While the rapid compression of biological materials may result in temperature increases of a few degrees (Fig. 5), the

increases are of short duration when the pressure vessel is submerged in a constant temperature water bath. The thermal time constant T-63 of aqueous solutions compressed in the steel pressure vessel is usually only two or three minutes; sometimes less than one minute. The rate of heat dissipation is influenced by ambient temperature, circulation of water in the bath, and by the heat capacity of the system.

DISCUSSION

Since it is difficult to predict or to duplicate all of the conditions affecting thermal changes in biological materials during compression or decompression, the magnitude and duration of such changes should be measured in experiments in which temperature may be critical in the intrepretation of results. Compressing physiological saline, common nutrient media, and similar aqueous solutions at 5 to 55°C to deep-sea pressures results in temperature increases ranging from 2 to 5°C. Decompression to atmospheric pressure results in equal cooling.

The magnitude of the thermal changes is influenced by the magnitude of the pressure change, ambient temperature, chemical composition of the system, and by other factors. Size, shape, and composition of the pressure vessel, its surroundings (temperature of air, water, etc.), and the rate of compression or decompression become significant factors to the extent that such experimental conditions affect the transfer or dissipation of heat. The rate at which heat is dissipated affects not only the magnitude of the thermal changes but also their duration in experimental materials. The thermal time constant T-63 in steel pressure vessels commonly employed for studying the effects of pressure on microbial activities ordinarily is only two or three minutes. Although the thermal changes and their duration may seem small, they have proved to be of critical importance in some of our work with thermolabile enzymes at deep-sea pressures to be reported in a subsequent paper.

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Spectrographic Analyses of Marine Plankton[1]

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ABSTRACT

The results of spectrographic analyses of ten species of zooplankton are presented. The methods used are described in detail. The elements determined quantitatively were boron, molybdenum, vanadium, nickel, cobalt, titanium, chromium, lead, tin, and copper. Manganese, cesium, rubidium, barium, strontium, and silver were detected in some or all of the specimens. Antimony, germanium, gallium, gold, and arsenic were sought for but not found. Cadmium was just detectable in only one species, the squid *Ommastrephes* (*Illex*) *illecebrosa*. The analytical results support the view that boron is actively concentrated or excluded by some marine animals. There is evidence that sedimentation of pteropod shells could be a major pathway for the removal of vanadium and lead from sea water. Lead was greatly enriched in *Centropages*. Nickel and cobalt showed random variations with respect to one another.

The elemental composition of marine organisms has interested chemists and biologists for a variety of reasons since before the nineteenth century, and an imposing amount of data has been accumulated. Most of the analyses obtained up to 1944, and some more recent, have been summarized and discussed by Vinogradov (1953). Unfortunately for those engaged in study of ecological or geochemical relationships in the oceans, or for those who wish to use such information to supplement physical oceanographic investigations, it appears that very few appropriate data exist. Not merely have few analyses been performed on species found in the marine plankton which represents, in spite of small individual dimensions, by far the major part of the biomass in the sea, but those few analyses which are available have often been made on specimens of uncertain provenance, and with methods of uncertain accuracy. We need a large number of analyses on simultaneously collected members of food chains, such collections being made often enough and from sufficiently varied localities, to permit comparative interpretation. Modern quantitative spectrographic techniques are capable of the required accuracy and precision when carefully controlled. They are the only techniques readily available that yield data, for large numbers of elements, on the small samples usually convenient for the marine biologist to collect in species purity high enough to permit the most complete interpretation.

The advent of atomic weapons testing has led to increased interest in the inorganic composition of marine organisms. Many marine plankters accumulate a variety of elements which may or may not have obvious biological significance. Some of these elements have radioactive isotopes which could eventually find their way into marine products of commerce, either directly or via food chains. Along these pathways the elements can be either concentrated or diluted depending upon the organisms involved.

In the most general sense, the presence or

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absence of a particular element in protoplasm has a "reason" behind it, and detection or lack of detection, particularly when very sensitive techniques are employed, permits us to construct hypotheses either about the chemical behavior of the organisms or about their environment.

The observations given in this paper are a part of a program instituted to study plankton ecology on the continental shelf of the northeastern United States (Ketchum *et al.*, 1957). This program is yielding data from bimonthly samplings at the same series of 22 stations, on the standing crop, rate of phytoplankton carbon fixation, and species composition of both phytoplankton and zooplankton communities. It appeared to us that data on the composition, for both major and minor elements, of as many as possible of the major plankton species would permit interesting geochemical interpretations. This report of our first series of analyses is intended to emphasize the practicality of moderately precise analyses by spectrochemical methods on very small samples, and the interest of the results so obtained.

It is a pleasure to acknowledge the assistance of Mrs. Doris Sutton in preparing the standard salt mixtures used.

METHODS

Collecting

The majority of the collections were conducted by towing a ¾-meter plankton net equipped with #2 nylon bolting cloth. The cod end consisted of a brass cup with monel metal screening and a rubber-stoppered outlet. All metal parts were coated with epoxyresin lacquer to prevent contamination of the sample. Tows were made at night when the deep scattering layer was near the surface, or when a just previous tow had revealed the presence of a desirable population. Large scyphozoans, salps, and ctenophores were collected with a dip net.

Collections were sorted, when necessary, but an effort was made to catch initially clean, pure species material. Each sample was drained on #2 bolting cloth and placed in a large porcelain crucible which had been cleaned with *aqua regia*. A few drops of 40 per cent solution of reagent-grade formaldehyde was stirred into each sample, and the crucible was then suspended over silica gel for preliminary drying on shipboard.

In the laboratory drying was continued *in vacuo* over silica gel. The samples were finally ashed to constant weight in a muffle furnace at 450°C to avoid loss of volatile components. Representative specimens of the species to be analyzed were prepared to obtain wet, dry, and ash weights.

The station locations for all the cruises have been described (Ryther and Yentsch 1958).

Data concerning the conditions and location of each collection are given in Table 1. It may be remarked that *Ommastrephes*, a squid, is by no means planktonic. However, it is included for the sake of comparison with other molluscs that are planktonic, and also because it was observed feeding extensively upon *Euphausia krohnii*.

TABLE 1. *Collection data for plankton samples analyzed spectrographically*

	Date	Time	Station	Collection
Euphausia krohnii Brandt	15 Jan. '57	2400	C	Surface tow
Berõe cucumis Fabricius	15 Jan. '57	2400	C	Surface tow
Centropages typicus (Lilljeborg) & *hamatus* Kroyer	17 Jan. '57	1800	A	Surface tow
Sagitta elegans Verrill	14 Feb. '57	0230	C	Surface tow
Calanus finmarchicus (Gunnerus)	22 Mar. '57	—	E	Surface tow
Salpa fusiformis Cuvier	24 Mar. '57	—	M	Surface tow
Calanus finmarchicus (Gunnerus) plus neritic phytoplankton	24 Mar. '57	0230	M	Surface tow
Limacina retroversa Fleming	29 Apr. '57	—	B	Surface tow
Cyanea capillata Eschschotty	29 Apr. '57	—	B	Dip net
Clione limacina (Phipps)	29 Apr. '57	—	B	Surface tow
Ommastrephes illecebrosa (Lesueur)	2 May '57	0001	H	Dip net

Analysis

A semi-quantitative total emission spectrographic procedure was used for the determination of the trace element contents of the ashed specimens.

A standard base, of composition 600 mg $CaCO_3$, 20 mg $MgCO_3$, 200 mg Na_2CO_3, 30 mg K_2CO_3, 65.5 mg H_2SiO_3, 100 mg Al_2O_3, was prepared. To this base varying amounts of compounds of a number of elements were added to give standards with a range of trace element contents from 5 to 500 ppm for most of the elements sought. For Ti the range was 10–500 ppm. Standards and ashed samples subsequently received identical treatment.

Two different arcing procedures were used, one for the relatively involatile elements B, Ti, V, Cr, Mo, Co, Ni, and the other for the volatile elements Pb, Sn, Cu, Cd.

For the involatile element determination the samples and standards were mixed with carbon powder in the ratio 1 part by weight sample (or standard) to 2 parts by weight carbon. Approximately 15 mg (actual weight recorded) of each carbon-sample or standard mix was loaded into a cylindrical cavity, 1.4 mm diameter and 7.1 mm deep, cut in the end of a carbon rod of diameter 3.2 mm. This loaded rod was made the anode of a DC arc, with a pointed carbon rod of diameter 4.2 mm forming the cathode. The arc was struck at 3 amp, and after 10 sec the current was raised to 6 amp and held there until the anode charge had been completely consumed (normally requiring 1 to 1½ minutes).

For the determination of the volatile elements a cooler arc is desirable. To achieve this, graphite electrodes were used, and the samples (and standards) were mixed with NaCl instead of carbon, 1 part by weight NaCl being added to 1 part by weight sample or standard. The dimensions of the graphite electrodes were the same as those of the carbon electrodes described above. Ten mg of sample-NaCl mix were loaded, the exact weight taken being recorded. The DC arc was struck at 3 amp, and after 1 minute the current was raised to 6 amp for a further 20 seconds, after which the arc was quenched. Preliminary examination had disclosed that emission of the volatile elements was complete in this time.

During all arcings an 8-stepped sector was interposed in the light beam before it entered a Hilger Fully Automatic Large Quartz and Glass Spectrograph. For the involatile elements a slit width of 0.30 mm was used, and for the volatile elements one of 0.45 mm. Spectra from the sample-carbon burns were recorded on Eastman Kodak 103-0 plates, those from sample-NaCl burns on Eastman Kodak 103a-0 plates. The plates were processed according to maker's instructions.

The lines used were:

B	2497.73 Å	V	3185.40 Å
Pb	2833.07 Å	Ti	3199.92 Å
Sn	2839.99 Å and 3175.02 Å	Cu	3247.54 Å and 3273.96 Å
Ni	3012.00 Å and 3414.76 Å	Co	3453.51 Å
Mo	3170.35 Å	Cr	4254.35 Å

Intensity measurements were made on each step of each line using a Hilger Hand-operated Microphotometer, and corrections were applied for background intensity. From the data obtained from the standards, working curves of log line intensity versus log concentration were constructed for several steps of each analysis line. From one arcing of an unknown sample the determination of line intensity in more than one step allowed more than one plot on the series of working curves. Such multiple plotting reduces the possibility of reporting aberrant results arising through local plate damage or inhomogeneity through error in a single measurement, and indicates the extent of error due to photographic recording (individual values range up to ± 10 per cent of mean value).

Where possible, replicate arcings were made, thus permitting an estimate of error due to variations in arcing conditions. In most cases this error exceeded that due to the use of photographic recording. An attempt to reduce the error was made by recalculating all intensities to a given weight of sample or standard in the electrode (4.5 mg in the same carbon burns, 5.0 mg in the sample-NaCl burns) on the assumption that the slope of the working curve had the theoretical value of 45°. This was not

notably successful and is not recommended in future work. Subsequent determinations of the slopes of the working curves indicated that they were frequently rather less than 45°, and this may help to explain the unsatisfactory results of the correction procedure.

The amount of some samples, *e.g. Clione*, was too small to permit multiple arcing, and the values for these samples (noted in the table by an asterisk) are thus somewhat less reliable than the others.

The working curves based on standards only extended up to 500 ppm. All values higher than this have been obtained by extrapolation and are thus less reliable the higher they are above this value.

Analysis for V has given some trouble, the only satisfactory standard available being that of 50 ppm. The working curve in this case was constructed by drawing the theoretical 45° line through carefully reproduced values on the satisfactory standard. Considering the range of sample values, this is unlikely to have introduced any large error—it may possibly have introduced a tendency for recorded values above 50 ppm to be slightly low and those below 50 ppm to be slightly high. Subject to these reservations, the errors involved are estimated where multiple arcings were possible, to amount in sum to ±30 per cent for boron and to ±15 per cent for the other elements reported.

At the time of making these analyses, suitable standards were not available for manganese, cesium, rubidium, barium, strontium, or silver. Lines of these elements do, however, appear in the spectrograms of some or all specimens. Standards are being prepared, and these values will be available for a subsequent report.

RESULTS

The analytical results are set out in Table 2 as parts per million of element in the ashed sample. For each specimen the per cent ash in the dry material (110°C) and the per cent dry weight of the fresh sample

TABLE 2. *Elements in plankton samples as parts per million of ash*

	Dry (% Fresh)	Ash % Dry	Ppm in Ash									
			B	Mo	V	Ni	Co	Ti	Cr	Pb	Sn	Cu
Coelenterata												
Cyanea capillata	4.6	63.0	100	3	5	<1	3	3	<1	6	4	13
Ctenophora												
Berŏe cucumis	4.7	70.3	115*	3*	8*	<1*	<1*	<1*	<1*	6*	7*	700*
Mollusca Pteropoda												
Limacina retroversa	18.7	64.2	50	8	85	2	20	5	<1	200	<1	30
Clione limacina	9.0	33.3	90*	<1*	16*	4*	30*	<1*		65*	20*	70*
Mollusca Cephalopoda												
Ommastrephes illicebrosa	22.7	7.7	420	4	4	<1	3	6	<1	5	3	2700
Arthropoda Copepoda												
Centropages typicus & hamatus	15.8	22.8	160	10	16	55	4	3	260	1300	50	600
Calanus finmarchicus	10.2	17.6	760*	12*	21*	165*	3*	10*		575	<1	1350
Calanus finmarchicus with ~ 50% neritic phytoplankton	12.2	36.3	325*	36*	54*	70*	80*	70*		75	90	300
Arthropoda Euphausiacea												
Euphausia krohnii	20.3	18.6	440	17	45	6	5	9	<1	20	<1	600
Chaetognatha												
Sagitta elegans	10.6	21.6	130	3	13	480	110*	3	<1	300	20	1100
Tunicata												
Salpa fusiformis	4.0	77.1	50	<1	7	60	<1	1	<1	3	8	500
Sea Salt	35.1		131[1]	0.4[2]	0.07[2, 3]	0.06[2]	0.007[3, 4]	0.20[2]	0.05[2]	0.11[1, 5]	0.09[4]	0.03[6, 7]

*—values based on a single arcing.
1—values taken from Kalle 1945.
2—values taken from Black and Mitchell 1952.
3—values taken from Ishibashi 1953.
4—value taken from Noddack and Noddack 1939.
5—value taken from Boury 1938.
6—value taken from Chow and Thompson 1952.
7—value taken from Morita 1953.

TABLE 3. *Spectrographic lines and estimated limits of sensitivity of analyses for elements sought but not found*

Spectra are from arcings for volatile elements.

Element	Wavelength of line Å	Limit of sensitivity ppm
As	2780.2	200
Au	2675.9	30
Ga	2934.6	3
Ge	2651.8	5
Sb	2877.9	100

are also presented. In addition to the ten elements shown in Table 2, antimony, germanium, gallium, gold, and arsenic were sought in each specimen, but not found. The estimated limits of sensitivity for these elements, with the methods used, are shown in Table 3. Cadmium was looked for despite the high (500 ppm) limiting sensitivity available. In the squid, *Ommastrephes*, cadmium was just detectable, whereas in all other specimens it was below the limit of detectability. The situation with respect to manganese, strontium, barium, silver, cesium, and rubidium has been discussed above in the section on methods.

For comparison we also present a compilation of the concentrations of the pertinent elements in sea salt, recalculated from sea water analyses of various authors, as listed. All values were normalized to 35.0‰ salinity, and calculated to ppm dry salt, taking Kalle's value of 35.141 g salt in 1000 g sea water of that salinity.

DISCUSSION

As we have stated above, few analyses of zooplankton are available. Those that can be cited offer some interesting comparisons.

Cyanea capillata was analyzed, also spectrographically, by the Noddacks (1939) for many of the same elements that we report. The two sets of analyses, as parts per million dry weight, are shown in Table 4.

The lack of correspondence between the two sets of values may reflect the fact that our specimens were caught well offshore, while theirs were from a landlocked fiord. It seems, however, quite as likely that organisms of very low ash-to-fresh-weight ratio, as coelenterates and ctenophores, exhibit a composition strongly reflecting that of recent food organisms. This point will require more observation. It is perhaps of interest that, with the exception of copper, our analyses for *Cyanea* and for *Beröe* agree quite closely. Unless we postulate for *Cyanea* an exceptionally slow regulation of Ti and of Sn, we do not know of any food organisms that might be responsible for such high values of these elements as were found by the Noddacks.

Calanus finmarchicus has been examined for element content by several workers, quoted by Vinogradov (1953). Our values (Table 5) indicate considerably greater enrichment of boron, nickel, and copper. Percentage-wise the nickel concentration is outstanding.

Although some assumptions have to be made about the composition of the phytoplankton contaminants, the analyses (Table 2) on *Calanus* plus 50 per cent phytoplankton, provide some support for the high nickel figure. Since the phytoplankton is unlikely to have been free of boron, lead, or copper, the values for the mixed sample may be taken to indicate that this *Calanus* population was lower in these elements, than was the pure. This is not surprising in view of Vinogradov's emphasis on the variability of total ash content of *Calanus* collections. With the exception of boron the general correspondence of values between *Calanus* and *Centropages* is quite good.

Ommastrephes has not previously been analyzed for any of the elements cited above, but our values show good correspondence with those cited (Vinogradov) for *Loligo:*

TABLE 4. *Comparison of analyses of Cyanea*

	Element ppm dry wt.								
	Mo	V	Ni	Co	Ti	Cr	Pb	Sn	Cu
Noddacks' value	2	5	30	7.1	6	1.3	27	32	68
Our value	1.9	3.1	0.6	1.9	1.9	0.6	3.8	2.5	8.2

TABLE 5. *Comparison of analyses of Calanus*

	Element ppm dry wt.					
	B	Mo	V	Ni	Ti	Cu
Vinogradov's values	71.6	0.6*	0.4*	0.12	6.4	present
Our values	134	2.1	3.7	29	1.7	238

* Values for *Carcinus maenas* (a benthic malacostracan, but the most closely related organism for which analyses could be found).

Cu, 200 ppm vs. 158; Mo, 0.3 vs. 0.3; and V, 0.3 vs. 0.4. As might have been expected, although the squids were caught when actively feeding on *Euphausia*; there is no striking correspondence of predator and food composition. No analyses for cadmium are reported for cephalopods, but Webb (1937) reported 10 to 400 ppm of ash in a variety of marine molluscs. It is thus too soon to say whether the high Cd of our *Ommastrephes* is a general molluscan character or the result of secondary concentration of the relatively high Cd of fish—one of the squid's major foods.

Intercomparison of the various specimens of Table 2 also yields some interesting points. Even though Webb (1937) had reported for marine molluscs a range of boron contents from 100 to 700 ppm of ash, Vinogradov (1953) postulated that boron, being a major ion of sea water and not of zoophysiological importance, could be used as an indicator of sea water equilibration. It is clear that our analyses are consistent with the range reported by Webb, and support the view that some marine animals actively concentrate this element, while others like *Limacina*, *Clione*, and *Salpa* must partially exclude it.

For molybdenum our uniformly rather high values for crustaceans are interesting, though not surprising in view of the indication that the phytoplankton mixed with one *Calanus* sample, was really quite rich in this element. There appears to be no evidence for such a connection of Mo and Cu as is reported for mammals (Marston 1952).

In the case of the two pteropods it is tempting to base comparisons on the presence of a shell in *Limacina* (highly phosphatic shell, according to Vinogradov and our own determinations) and the absence of any shell in *Clione*. Should this be a reasonable basis for comparison, Mo, V, Pb, and possibly Ti are indicated as strongly enriched in the pteropod shell, V and Pb so much so that sedimentation in this way might be estimated to be a major pathway of removal of these elements from the sea.

The random variation of nickel and cobalt with respect to each other is quite striking. No support appears for the sort of phylogenetically regular Ni:Co ratios that were postulated by Bertrand and Macheboeuf (1925). Both pteropods and the squid agree in being exceptions to Vinogradov's generalization that in Mollusca nickel is found more frequently than cobalt and in larger quantities. Reasonable assumptions about ash weight:dry weight ratios, applied to the nickel analyses reported by Laevastu and Thompson (1956) for several mixed plankton hauls, indicate adequate agreement between our crustacean data and theirs. Very possibly, nickel accumulation will prove to be typical of copepods. The enormous values for Ni and Co for *Sagitta* interest us considerably. It should, however, be noted that because of its higher total ash content, *Limacina* proves to concentrate Co on a fresh weight basis, to the same extent that *Sagitta* does. This illustrates a pitfall of working from ash or dry weight concentrations only.

The very wide range of concentrations of lead is striking. It is interesting to note that Vinogradov had suspected a reported value of 25 ppm (dry) in lobster, as improbably high. Our value of 1300 ppm (ash) for *Centropages* presents some problems of physiological interpretation. We hope that parallel data for silver, and analyses of phytoplankton blooms for both elements, will help to clear up this.

We believe the high values for Ti and Sn in the *Calanus*-plus-phytoplankton sample are likely to represent silt particle collection in a rather turbid coastal water. It is, however, clear that considerable amounts of these, often called bio-inert, elements are commonly retained by phytophages, and even by such secondary predators as *Cyanea* or *Ommastrephes*. Their

cycles in the sea will surely prove to have considerable contribution from biological processes.

The relatively few analyses herein presented clearly demonstrate the need for many more. For subsequent geochemical applications it is essential that a variety of elements should be sought in the same organism and this requirement suggests a spectrographic method of analysis. In this exploratory work a rapid, semi-quantitative method was used. The results obtained indicate that internal standardization techniques with greater analytical precision would certainly prove worth while, and we intend to adopt them in our future work. Most generalizations that might have been indicated by previous studies prove not to hold, and the picture of the diversity of chemical behavior among the members of plankton communities is most striking. Certainly the safest generalization promises to be that for any given chemical element there will eventually be found at least one plankton species capable of spectacularly concentrating it.

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The Respiration of Some Planktonic Copepods

III. The Oxygen Requirements of Some American Species

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ABSTRACT

The respiratory rates of two neritic planktonic copepods, *Centropages hamatus* and *Temora longicornis* obtained from the northeast coast of the United States, have been shown to be very similar to the rates determined for British specimens, provided due allowance is made for the difference in size of the animals.

The relationship previously suggested between respiratory rate and length for planktonic copepods, appears to hold for these two American species, but in the case of *Temora* the modified formula suggested by Gauld and Raymont (1953) must be used. The relationship applies also to *Pseudocalanus minutus*. *Tortanus discaudatus* has been found to have a higher rate as determined experimentally. It is suggested that this high rate is associated with the carnivorous feeding of this copepod.

Experiments on the respiration of *Eurytemora herdmani* show that females have a considerably higher oxygen demand than males, though the difference becomes only slight when due allowance is made for the difference in size between the sexes. Some experiments conducted on the respiratory rates at 15° and 20°C suggest that *Eurytemora herdmani*, in contrast to the other calanoids investigated, does not show any increase in respiratory rate beyond 15°C.

In the laboratory lack of feeding in *Tortanus* is associated with a marked decline in respiratory rate; to a lesser extent a reduction in respiration with lack of food has been observed in *Centropages hamatus*.

INTRODUCTION

Interest in the respiratory rate of marine plankton has largely centered around the metabolic requirements of copepods—one of the most important members of the zooplankton community. However, as Marshall and Orr (1955) have stressed, the number of investigations is small, and the different techniques which have been employed make it somewhat difficult to assess the significance of the results. Undoubtedly the best known species is *Calanus finmarchicus* (cf. Marshall *et al.* 1935; Marshall and Orr 1955, 1958), and some comparative data are available for the respiratory rate of this species from American waters (Clarke and Bonnet 1939). There are very few other comparative data for the respiration of calanoids from European and American coasts. Conover (1956) investigated the respiration of *Acartia clausi*, and this species had already been examined by Gauld and Raymont (1953).

It seemed desirable, since Raymont and Gauld (1951) and Gauld and Raymont (1953) had already obtained some measurements on the respiratory rates of some small neritic calanoids from Britain, to measure the respiration of similar neritic species from the northeast American coast using the same manometric method. Unfortunately some of the neritic species were not obtainable at the time of experimentation, but a few comparisons may now be attempted, and some data are also presented for the respiration of calanoids that are exclusively American.

MATERIALS AND METHODS

The work was carried out during April and May at the Biological Laboratories, Harvard University. Some of the material was obtained by hand towing plankton nets off local beaches near Boston; other material was obtained off Woods Hole Dock and was sent to Harvard, usually within 24 hours. In the laboratory the catches were diluted with filtered sea water, large predators such

as ctenophores removed, and the plankton stored in breffits in a cold room (7° to 8°C). Uni-algal phytoplankton cultures (*Dunaliella*, *Dicrateria*, and *Isochrysis*) were added as food.

The calanoids selected for experiment were sorted from the stock breffits as soon as possible. Many were sorted the same day, but some of the material was not used until a week or more after capture. In general the calanoids survived fairly well under laboratory conditions. The animals were first transferred to crystallizing dishes (200-ml capacity) containing filtered sea water, to which the same phytoplankton food cultures were added. They were then returned to the cold room and were kept at least overnight (often 1 to 2 days) before using for the respiratory determinations. This practice was followed in an attempt to avoid the raised respiratory rate that can occur for the first 24 hours or so after capture due apparently to the handling (cf. Gauld and Raymont 1953).

As far as possible selection of the copepods from the stock breffits was made by eye. At the conclusion of an experiment the animals were transferred from the respirometer flasks to a dish of sea water and any dead or unhealthy specimens noted. The copepods were then fixed in 5% formalin and the identifications later checked under a binocular microscope. The length of the cephalothorax of all fixed animals used in each experiment was measured with a micrometer eyepiece, and the number of copepods checked against the initial number. However, in a few cases only a portion of the animals employed were measured, and the initial number was then taken in calculating the respiratory rate. Occasionally, with sorting by eye, an animal other than the species desired was found to have been included in an experiment. Only in the case of some of the *Eurytemora* experiments, however, was there any serious mixture of species; these experiments were rejected (*vide infra*).

The respiration measurements were made in Barcroft-Dixon constant pressure manometers (Raymont and Gauld 1951). Five ml sea water were used in each flask; the number of copepods varied according to the species. The measurements were conducted in the laboratory, but the bath containing the respirometer flasks was maintained at fairly constant temperature by means of a cooling unit and heater relay system. In some of the earlier experiments there was as much as ±0.5°C variation in temperature owing to imperfect mixing of the bath contents, but later on this variation was reduced. In any event it is highly unlikely that this variation had any noticeable effect on the respiratory rate. Most of the experiments were conducted at either 15° or 20°C. The flasks were shaken at a speed of 60 oscillations per minute. Experiments normally ran for three hours, after an equilibration period of 15 minutes, and several readings were always made during the course of a run. The total gas change was converted to volume of dry gas at N.T.P. In a very few runs there was no change in gas volume or irregular change owing to leakage, and such results have been disregarded.

RESULTS

1. *Tortanus discaudatus* (Thompson & Scott)

This species, though a well known American neritic calanoid, is not found in British waters, and no data are available for its respiration.

Usually 15 to 20 copepods were used in one experiment, but as the species was never abundant in the plankton, males and females and an occasional Stage V were used together. However in several experiments one sex was markedly predominant, and it appeared from these that females had a somewhat higher respiratory rate than males (average 0.366 μLO_2/cop./hr for females; 0.281 for males; at 15°C). But female *Tortanus* are larger than males. A correction was applied for this size difference, the rate being regarded as proportional to surface area, reckoned as the square of the cephalothorax length (Raymont and Gauld, 1951). The corrected respiratory rates then showed very little difference between the sexes. The mean rate at 15°C for all *Tortanus* combined was 0.275 μLO_2/cop./hr

(Table 1). Probably Experiment No. 68 should be excluded as, by mistake, more copepods than usual were used in the respirometer flask, and the crowding appears to have depressed the rate markedly. The mean rate, excluding Experiment No. 68, is 0.288 ± 0.023. The few experiments conducted at 20°C suggest a slight rise in respiratory rate with temperature (mean 0.324 ± 0.024: Table 1).

Tortanus appears to be very sensitive to laboratory conditions. The experiments listed in Table 1 were all conducted on material collected off beaches near Boston and used within 1 to 2 days. Plankton hauls from Woods Hole were used successfully over several days for other copepods (*e.g.*, *Centropages*, *Pseudocalanus*), but *Tortanus* kept under the same conditions gave low respiratory rates and rapidly died. On one occasion *Tortanus* were kept for three days after capture and a respiratory determination then made. The rate was 0.10 μLO_2/cop./hr—approximately one-third of the normal rate. The copepods were still alive, though sluggish, and two further tests were made on the same animals. On the second run the rate dropped to 0.06 μLO_2/cop./hr, and in the final run there was no measurable respiration though the animals were all alive.

There is some evidence that this tendency to a sharp reduction of respiratory rate in *Tortanus*, accompanied by general low activity in the laboratory, is correlated with lack of feeding. Although cultures of *Dunaliella*, *Dicrateria*, and *Isochrysis* were offered to these copepods, no real feeding was observed. After being kept overnight or even longer in such food cultures, collections of healthy *Tortanus* showed practically no faecal pellet production, although other calanoids (*Pseudocalanus*, *Temora*, *Eurytemora*) showed extensive feeding. At the most, only 1 or 2 faecal pellets were recovered from dishes containing *Tortanus*, and normally the copepods showed no green food in the gut. On many occasions eggs were found from adult cultures, and in a few cases where Stage V copepodites were used some of these proceeded to the moult stage, but in no case was feeding on phytoplankton evident. Once a female was seen to feed on a moribund male specimen. The

TABLE 1. *Respiratory rates for Tortanus discaudatus*
Grand mean length 1.239 mm.

Temp. (°C)	Expt. No.	No. of animals	Mean length (mm)	Uncorrected respiration rate (μLO_2/cop./hr)	Corrected respiration rate
15°	15.2	1	15^{-1}	1.395	0.435	0.343
	15.2	2	16	1.441	0.294	0.217
	15.2	4	15^{-1}	1.253	0.352	0.344
	15.4	5	18	1.245	0.202	0.200
	15.4	6	11^{-2}	1.334	0.242	0.209
	15.2	10	20	1.418	0.368	0.281
	15.2	11	18	1.281	0.346	0.324
	15.5	66	15^{-1}	1.097	0.224	0.286
	15.5	67	17	1.052	0.279	0.388
	15.0	68	25^{-1}	1.153	0.133	0.154
					Mean	0.275 ± 0.024
20°	20.0	61	20	1.215	0.301	0.314
	20.0	62	18^{-1}	1.204	0.348	0.369
	20.0	63	19	1.132	0.240	0.288
					Mean	0.324 ± 0.024

Note. In this and the following tables, any copepods dying during an experiment are noted by a figure subtracted from the total used.

In all the Tables the corrected respiration rate has been calculated as proportional to $\frac{(Lm)^2}{L^2}$ where Lm = grand mean cephalothorax length of all specimens, and L = mean cephalothorax length for the one experiment.

male was held firmly by the female, and after several minutes only a "husk" of cuticle remained. Fragments of individuals were recovered in one or two other dishes. Johnson (1934) also found no evidence of *Tortanus* feeding on mixed diatom cultures in his rearing experiments, but he was able to feed young stages on copepod larvae. Bigelow (1926), Lebour (1922), and others have shown that some copepod species feed partly on other zooplankton, but it would appear that *Tortanus* is almost wholly carnivorous. The sharp drop in respiratory rate in the laboratory may be associated with a lack of suitable animal food.

2. *Centropages hamatus* (Lilljeborg)

All *C. hamatus* material came from Woods Hole collections. Both males and females were employed but, except for Experiment No. 9 (Table 2), immature copepodite stages were not used apart from the accidental inclusion of an individual. Approximately 35 to 40 animals were used in each experiment. Survival was good; thus out of more than 20 experiments altogether only 3 copepods died during the course of the experiments. In several cases animals were tested in respirometers more than once (Table 3).

The size range was from as little as 0.8 mm for a few males to a maximum of 1.3 mm for some females. The mean length for all experimental animals was 1.06 mm, and the respiratory rates have therefore been corrected for the varying size of the copepods employed in a run according to the square of the mean length (Table 2). At 15°C the mean respiratory rate was 0.137 μLO_2/cop./hr as against 0.172 μLO_2/cop./hr at 20°C, though both sets of experiments showed a fairly wide range (Table 2).

A few experiments were carried out with *Centropages hamatus* in an attempt to test the effect of feeding on respiratory rate. In these tests, before the determinations of respiratory rates were made, copepods were transferred to dishes containing either filtered or sterile sea water and were given no food for periods of 2 to 3 days, while control animals were fed in the usual manner. Examination of the "unfed" cultures showed either no faecal pellets, or (in the case of those in filtered sea water) a few, very pale pellets. This very limited feeding was possible as a few μ-flagellates, naturally present in the sea water, passed through the filter paper.

Respiratory rates on the "unfed" copepods

TABLE 2. *Respiratory rates for Centropages hamatus*
Grand mean length 1.061 mm.

Temp. (°C)	Expt. No.	No. of animals	Mean length (mm)	Uncorrected respiration rate (μLO_2/cop./hr)	Corrected respiration rate
			Fed copepods		
	15.0	9	44	1.078	0.149	0.145
	15.0	12	35	1.101	0.213	0.198
15°	15.0	18	38	1.071	0.133	0.131
	15.1	28	38[-1]	1.143	0.102	0.088
	15.0	32	19	1.078	0.128	0.124
						Mean 0.137 ± 0.018
	20.0	37	39	1.000	0.192	0.216
20°	20.0	38	38	1.002	0.173	0.194
	20.0	39	38	0.978	0.102	0.120
	20.0	42	40	1.057	0.156	0.157
						Mean 0.172 ± 0.021
			Unfed copepods		
	15.0	19	40	1.105	0.131	0.121
15°	15.1	29	42	1.088	0.050	0.048
	15.0	33	22	1.118	0.097	0.087
						Mean 0.085 ± 0.021

TABLE 3. *Respiratory rates for Centropages hamatus—repeat experiments*
Grand mean length 1.061 mm.

Temp. (°C)	Expt. No.	No. of animals	Mean length (mm)	Uncorrected respiration rate (μLO_2/cop./hr)	Corrected respiration rate
15° 14.9	22	37	1.071	0.041	0.040
14.9	23	36	1.113	0.051	0.046
					Mean 0.043 ± 0.003
20.0	44	38	0.996	0.047	0.054
20.0	45	37	0.977	0.049	0.058
20° 20.0	46	36[-1]	0.998	0.067	0.076
20.0	47	39	1.012	0.085	0.094
20.0	48	39	1.067	0.101	0.100
					Mean 0.076 ± 0.009

showed a marked drop. At 15°C there was a mean rate of 0.085 μLO_2/cop./hr, as compared with the usual rate for fed individuals of 0.137 μLO_2/cop./hr (Table 2). The precise effect of feeding on respiratory rate is difficult to assess, however, as in the normal "fed" cultures it appeared on some occasions that feeding (as reckoned from faecal pellet production) was less active than expected. Normally the dishes would be covered with faecal pellets, but on some occasions relatively few were produced, though there were *always* far more than in "unfed" cultures. Part of this reduction in feeding may possibly be due to age of food culture since a standard age was not employed. However, it occurred sometimes with young food cultures. Also, other copepods (especially *Pseudocalanus*) given identical cultures at the same time always fed extremely actively. There is a suggestion (Lebour 1922) that *Centropages typicus* is partly carnivorous, and this may be true then of *C. hamatus*.[1] Possibly therefore the occasional reduction in active feeding was a reflection of need for some food other than phytoplankton.

There is another complicating factor in the respiration of *Centropages*. Previous work (Raymont and Gauld 1951, Gauld and Raymont 1953) has demonstrated both for *C. typicus* and *C. hamatus* rather wide ranges in respiratory rate. In the case of *C. typicus* (Raymont and Gauld 1951) it was suggested that this might be partly due to handling in the laboratory. A few experiments were carried out in which specimens of *C. hamatus*, which had already been satisfactorily used for a respiratory run, were transferred overnight to a fresh dish of sea water containing food and then used for a second respiratory rate determination. Examination of the dishes in such cases showed some faecal pellets but the numbers were always markedly low. It should be emphasised that all the animals appeared very active and healthy, and on several occasions numbers of eggs were laid in the dishes, but feeding was greatly reduced.

The respiratory rates obtained in these Repeat Experiments (Table 3) were also much lower than expected. Thus at 20°C the mean corrected rate was 0.076 μLO_2/cop./hr (Table 3) as against a mean of 0.172 μLO_2/cop./hr for animals used once only, *i.e.*, approximately only 44%. Only two Repeat Experiments were carried out at 15°C (Table 3), but there was again a marked reduction—mean rate 0.043 μLO_2/cop./hr as compared with 0.137 μLO_2/cop./hr, *i.e.*, ca. 31%. There appears then to be a sharp drop in respiratory rate when *C. hamatus* is repeatedly handled in the laboratory, and this is associated with a decline in feeding.

3. *Pseudocalanus minutus* (Krøyer)

A few *Pseudocalanus minutus* were obtained from both Woods Hole and beaches near Boston. This species appeared to survive comparatively well under laboratory

[1] A specimen of *Centropages hamatus* has recently been observed in the laboratory at Southampton feeding on *Acartia* (Lance, unpublished).

TABLE 4. *Respiratory rates for Pseudocalanus minutus*
Grand mean length 0.984 mm.

Temp. (°C)	Expt. No.	No. of animals	Mean length (mm)	Uncorrected respiration rate (μLO_2/cop./hr)	Corrected respiration rate
			Fed copepods		
15.2	13	40	1.127	0.102	0.078
15.2	14	45	0.979	0.076	0.077
14.8	16	50	0.957	0.087	0.092
15° 14.8	20	46	0.952	0.123	0.132
14.7	30	46	0.993	0.093	0.091
14.9	34	50	0.938	0.119	0.131
14.9	35	50	0.963	0.119	0.124
					Mean 0.104 ± 0.009
20° 20.0	36	50	0.964	0.133	0.139
			Unfed copepods		
15° 14.8	21	47	1.012	0.127	0.120
14.8	31	42	0.985	0.080	0.080
					(?) Mean 0.100 ± 0.020

conditions and fed actively on phytoplankton cultures. There was invariably an abundant production of faecal pellets in cultures containing this calanoid.

Both males and females were used for respiratory rate determinations. In general males were somewhat smaller: in Experiment No. 16, where almost all specimens were male, the mean length was only 0.957 mm, whereas Experiment No. 13 (all females) gave the greatest mean length (1.127 mm). However, even the females showed considerable size variation: Experiment No. 20 gave a mean length of only 0.952 mm and Experiment No. 35, 0.963 mm, though both experiments consisted almost solely of females. The respiratory rates for all experiments have therefore been corrected to a grand mean length of 0.984 mm (Table 4). At 15°C the mean respiratory rate amounted to 0.104 μLO_2/cop./hr.

It was hoped to compare this normal rate with that of unfed *Pseudocalanus* (cf. *Centropages* experiments) and also to test the effect of temperature, but unfortunately this calanoid disappeared from the plankton hauls from Woods Hole after only a few preliminary runs had been completed. The results of these few tests are however suggestive. Thus in two experiments (No. 21 and 31) female *Pseudocalanus* were kept in filtered sea water for 2 and 5 days, respectively. A few small μ-flagellates were present in the filtered water, and a very few pale faecal pellets were obtained from each culture. Feeding, however, was markedly reduced, as compared with controls fed on *Dunaliella* and *Dicrateria*. The respiratory rates for these two experiments were 0.120 and 0.080 μLO_2/cop./hr, respectively, *i.e.*, well within the range for normally fed copepods, and the difference in the mean rates for fed and unfed animals is not significant (Table 4). This preliminary result would suggest that even a very low rate of feeding is sufficient to maintain the respiratory rate in *Pseudocalanus*, a conclusion in contrast to that for *Centropages*.

Only one experiment on *Pseudocalanus* was carried out at 20°C. The corrected respiratory rate was 0.139 μLO_2/cop./hr (Table 4), suggesting an increase in rate with temperature. A few animals were used in repeat runs, and, as for *Centropages*, there appeared to be a reduced respiratory rate. These results have not been included in Table 4.

4. *Eurytemora herdmani* Thompson & Scott

This calanoid was obtained in some numbers from one plankton haul made off Revere Beach, Boston, on the 11th of May. A few specimens were also obtained in a

collection off Nantasket and were used in one experiment, but all other experiments were made on the first collection. No further *Eurytemora* could be obtained, and none were taken from Woods Hole hauls, so that only preliminary results can be given.

Eurytemora survived well, feeding actively on the phytoplankton cultures and producing masses of faecal pellets. An indication of the healthy condition of the cultures was that many of the specimens used were ovigerous females, and in a number of cases active nauplii were hatched from the eggs. An attempt was made to sort female ovigerous *Eurytemora* from males merely by eye so that the respiration of males and females could be compared. Unfortunately it was found when the specimens were checked under a microscope after an experiment that in a number of experimental runs some *Eurytemora hirundoides* had been included and, on one or two occasions, some other copepods. In Table 5 only those experiments are quoted where not more than one or two copepods out of a total of 40 or 50 belonged to any species other than *Eurytemora herdmani*.

The grand mean length for all *Eurytemora* used in the experiments was 0.799 mm; females were generally larger than males (mean length for females, 0.859 mm; mean length of males, 0.752 mm). There was a considerable spread in the respiratory rates obtained, and as the average size also varied a correction was made for size on the basis of the square of the mean length (Table 5).

At 20°C the mean corrected respiratory rate was 0.100 μLO_2/cop./hr; at 15°C the mean rate was 0.104 μLO_2/cop./hr (Table 5). This would suggest no increase in respiration from 15°C to 20°C, a result which is somewhat surprising. Experiment No. 54 at 20°C (Table 5) should, however, perhaps be excluded as it differed from the rest in that there was a large proportion of Stage V *Eurytemora* which were not used in any other experimental run. In the group of experiments at 15°C also there is one experiment (Experiment No. 78) which should be excluded. On re-examination of the material it was found that no fewer than eight of the specimens belonged to copepods other than *Eurytemora*.

The mean respiratory value at 20°C excluding Experiment No. 54 remains however at 0.100 μLO_2/cop./hr; that at 15°C excluding Experiment No. 78 is 0.106 μLO_2/cop./hr. In fact, therefore, the exclusion of the two experiments does not affect materially the conclusion advanced before, *i.e.*, that the mean respiratory rates at 20°C and at 15°C appear to be the same.

It was decided to separate the experiments on male and female specimens in order to

TABLE 5. *Respiratory rates for Eurytemora herdmani*
Grand mean length 0.799 mm.

Temp (°C)	Expt. No.	No. of animals	Mean length (mm)	Uncorrected respiration rate (μLO_2/cop./hr)	Corrected respiration rate
15.0	73	44	0.872	0.153	0.128
15.0	74	50	0.762	0.085	0.094
15° 15.0	76	59	0.752	0.103	0.117
15.0	77	55	0.755	0.078	0.087
15.0	78	40	0.888	0.117	0.095
					Mean 0.104 ± 0.008
19.7	50	50	0.907	0.153	0.118
19.7	51	50	0.813	0.181	0.174
20.0	54	50	0.745	0.084	0.096
20.0	55	50	0.744	0.102	0.117
20° 20.0	56	50	0.835	0.097	0.089
20.0	57	50	0.745	0.0535	0.0615
20.0	58	55	0.857	0.126	0.109
20.0	59	56	0.748	0.062	0.0705
20.0	60	55	0.836	0.070	0.064
					Mean 0.100 ± 0.012

TABLE 6. *Respiratory rates for male and female Eurytemora.* Grand mean length 0.799 mm.

Temp. (°C)	Expt. No.	Mean length (mm)	Uncorrected respiration rate (μLO_2/cop./hr)	Respiration rate corrected to mean length of sex	Respiration rate corrected to grand mean length
			Males	♂♂ (0.752 mm)	
	55	0.744	0.102	0.104	0.117
20	57	0.745	0.0535	0.0545	0.0615
	59	0.748	0.062	0.063	0.0705
			Mean 0.073 ± 0.015	0.074 ± 0.015	0.083 ± 0.017
	74	0.762	0.085	0.083	0.094
15	76	0.752	0.103	0.103	0.117
	77	0.755	0.078	0.077	0.087
			Mean 0.089 ± 0.007	0.088 ± 0.008	0.099 ± 0.009
			Females	♀♀ (0.859 mm)	
	50	0.907	0.153	0.137	0.118
	51	0.813	0.181	0.202	0.174
20	56	0.835	0.097	0.103	0.089
	58	0.857	0.126	0.127	0.109
	60	0.836	0.070	0.074	0.064
			Mean 0.125 ± 0.020	0.129 ± 0.021	0.111 ± 0.018
15	73	0.872	0.153	0.149	0.128

compare their respiration rates. The uncorrected respiratory rates are much less for males than for females; at 20°C, for example, the mean is 0.125 μLO_2/cop./hr for females as against 0.073 for males (Table 6). Female *Eurytemora* averaged 0.859 mm in length, and the respiratory rates obtained for experiments on females have been corrected to this mean length. The average respiratory rate at 20°C is 0.129 μLO_2/cop./hr (Table 6). In the case of males (0.752 mm mean length) the corrected mean result at 20°C is 0.074 μLO_2/cop./hr (Table 6). The difference is largely due to the discrepancy in size between the sexes. When the respiratory rates for both sexes are corrected to a grand mean length for all specimens (0.799 mm) the rate at 20°C is 0.111 μLO_2/cop./hr for females and 0.083 for males. With so few determinations the standard errors of the means are large (Table 6). There is nevertheless some suggestion that, apart from length, the respiratory rate of females is somewhat greater. This may be partly due to the fact that a large percentage of females were carrying egg sacs, and no correction was made for the respiration of the ova. Furthermore female *Eurytemora herdmani* are characterized by large posterior flanges at the end of the metasome, and no allowance was made in the measurements for this increased surface.

No close comparison of the respiratory rates of males and females can be made for the lower temperature (15°C). It is perhaps, however, worth noting that there is no decrease in respiratory rate at the lower temperature for either sex; indeed there is some suggestion of a slightly increased respiration at 15°C for males (Table 6).

5. *Temora longicornis* (Müller)

This calanoid was obtained in small numbers only. It survived well in the laboratory, feeding very actively on algal cultures and producing eggs. Owing to the few specimens available, only 3 runs, all at 15°C, were completed. The mean respiratory rate for males and females combined was 0.140 μLO_2/cop./hr. The average size of those animals used in Experiment No. 70, however, was distinctly smaller, and therefore the rates in all three experiments have been corrected to a mean length of 0.965 mm. The mean respiratory rate is then slightly higher—0.147 μLO_2/cop./hr (Table 7).

6. *Centropages typicus* Krøyer

This species was never common in the hauls, and only one collection (from Nantas-

TABLE 7. *Suggested respiratory rates for Temora, Centropages typicus and Metridia.*
Grand mean length *Temora longicornis* 0.965 mm.
Grand mean length *Centropages typicus* 1.0195 mm.

Temp. (°C)	Expt. No.	No. of animals	Mean length (mm)	Uncorrected respiration rate (μLO_2/cop./hr)	Corrected respiration rate
			Temora longicornis		
14.8	17	29	0.965	0.161	0.161
14.9	26	50	1.040	0.116	0.100
15.0	70	35	0.859	0.142	0.179
				(?) Mean	0.147
			Centropages typicus		
15.0	69	35[-1]	0.942	0.105	0.123
15.0	71	34	1.097	0.221	0.191
				(?) Mean	0.157
			Metridia lucens		
15.5	64	14	1.384	0.336	—
15.5	65	10	—	0.294	—
				(?) Mean 0.315	

ket) had sufficient specimens for experiment. Even then males, females, and Stage V had to be used together. As there was some difference in the average length of *Centropages* in the two runs, the respiratory rates have been corrected to a mean length of 1.019 mm; the average respiratory rate was then 0.157 μLO_2/cop./hr at 15°C (Table 7).

7. *Metridia lucens* Boeck

A few specimens of this well known calanoid were obtained once, and the results of two experiments (Table 7) are included to indicate the probable order of magnitude of the respiratory rate. All the specimens obtained were Stage V copepodites. They were kept for several days in the laboratory and fed very actively on *Dunaliella*. The results (Table 7) suggest a respiratory rate of ca. 0.315 μLO_2/cop./hr at 15°C.

DISCUSSION

Comparison of the respiratory rates of marine planktonic copepods of the same species but taken from different areas is complicated by such factors as size, degree of maturity, and generation. Variation with the seasons has also been suggested (Gauld and Raymont 1953, Conover 1956, Marshall and Orr 1958), though the effects due to size alone, which also varies with the season, must be taken first into consideration. Thus it appeared that with *Calanus* the respiratory rates obtained by Clarke and Bonnet (1939) and by Raymont and Gauld (1951) were somewhat higher than those found by Marshall *et al.* (1935). Since Clarke and Bonnet obtained their higher results by both manometric and Winkler methods the differences were probably not attributable to method. The recent demonstration by Marshall and Orr (1958) of the effect of season on oxygen consumption in *Calanus* makes it probable, however, that the differences may be largely due to this factor. In any event, as Marshall and Orr have already stated, the differences between the results of the three investigations were not large.

In the case of neritic calanoids it would appear that the respiration has been studied on both sides of the Atlantic only in the case of *Acartia clausi*. Gauld and Raymont (1953) obtained a mean rate for British (Southampton) *Acartia clausi* of about 0.08 μLO_2/cop./hr at 17°C. Conover (1956) obtained lower rates for specimens from North America (Long Island Sound): at 15°C about 0.04 to 0.02 μLO_2/cop./hr. Conover obtained an increase in rate with temperature, but his curve suggests an oxygen uptake even at 17°C of not more than 0.04 μLO_2/cop./hr. It was suggested by Conover that the smaller size of the *Acartia* from Long Island Sound may have accounted for the lower respiratory values. However, the mean length of Long Island

Sound specimens was 0.75 mm (Conover 1956), whereas the British specimens had a mean length of 0.85 mm (Gauld and Raymont 1953). Thus Conover's copepods were not so very much smaller than the Southampton *Acartia*, and the difference in respiration cannot certainly be attributed to size alone.

Conover (1959) has criticised the manometric method, since there are fluctuations in rate as determined by half-hourly readings which he believes are largely attributable to temperature variations affecting the mercury column of the manometer which is not housed in a constant temperature bath. Conover did obtain a rather larger standard error from manometer experiments than in Winkler experiments on the respiration of *Acartia*. Nevertheless the mean rate as determined by both methods on Southampton specimens in general confirmed the high values obtained previously for British *Acartia*. Recent experiments at Southampton on other zooplankton have also suggested that the Winkler and Haldane-Dixon manometric methods give fairly comparable results.

In the experiments now reported, in order to avoid confusion due to different methods the same Haldane-Dixon manometric technique has been employed as previously by Raymont and Gauld (1951) and Gauld and Raymont (1953).

A comparison may first be made for *Centropages hamatus*. The oxygen requirements found for American (Woods Hole) copepods were 0.137 μLO_2/cop./hr at 15°C and 0.172 μLO_2/cop./hr at 20°C. At 17°C the rate would be ca. 0.151 μLO_2/cop./hr. The oxygen requirement of these *Centropages* from Woods Hole is considerably above that quoted by Gauld and Raymont (1953) for *Centropages hamatus* from Southampton Water (0.082 μLO_2/cop./hr at 17°C). The difference, however, is partly due to the smaller size of the Southampton specimens (average length 0.882 mm). If we apply a correction for size, using L^2 as a rough approximation for surface area, and calculate the respiratory rate of British (Southampton) *Centropages*, if their mean length were equal to that of North American specimens (*i.e.*, 1.061 mm) we obtain the following:

$$R = \frac{(1.061)^2 \times 0.082}{(0.882)^2} = 0.119.$$

That is, their respiratory rate would be 0.119 μLO_2/cop./hr at 17°C, as compared with the rate of 0.151 μLO_2/cop./hr for American specimens.

Though very few results are available for the related *Centropages typicus* a brief comparison may be made. A respiratory rate of 0.157 μLO_2/cop./hr at 15°C has been given for American *C. typicus* (Table 7). Earlier determinations on British specimens suggested that the results fell into two groups with means of 0.268 and 0.161 μLO_2/cop./hr at approximately 16°C.

The value for the American specimens appears to be low, but the mean size of the copepods used is very different. The average length of female British *Centropages typicus* with the respiratory rate of 0.268 μLO_2/cop./hr was 1.25 mm. The mean length of the North American specimens is only ca. 1.02 mm owing largely to the inclusion of a number of Stage V copepodites. However, the respiratory rate for the North American copepods may be calculated for an average length of 1.25 mm, using again L^2 as an approximation to surface area. Thus:

$$R = \frac{(1.25)^2 \times 0.157}{(1.02)^2} = 0.236.$$

The calculated rate (0.236 μLO_2/cop./hr) falls therefore between the values given for British specimens, though it is much closer to the higher rate.

The respiratory rate of British specimens of *Temora* from Southampton Water was determined by Gauld and Raymont (1953) as 0.108 μLO_2/cop./hr at 17°C, equivalent to ca. 0.093 μLO_2/cop./hr at 15°C. This may be compared with the rate now quoted of 0.147 μLO_2/cop./hr at 15°C for *Temora* from North American coasts. The marked difference may be accounted for again by the considerable difference in mean size of the *Temora* populations: British specimens averaged 0.787 mm; the North American

Temora, 0.965 mm. If we calculate the value of the respiratory rate for American specimens of the same mean size as British (Southampton) *Temora*, using L^2 as a rough approximation for surface, we obtain the following:

$$R = \frac{(0.787)^2 \times 0.147}{(0.965)^2} = 0.098.$$

That is, at 15°C American and British specimens of the same average length (0.787 mm) would have respiratory rates of 0.093 and 0.098 $\mu L O_2$/cop./hr, respectively—an extraordinarily close agreement.

Comparative figures are not available for the respiration of *Pseudocalanus* and *Metridia* from British waters, but as both species are important calanoids on both sides of the Atlantic a full investigation is desirable. No comparison can be attempted for *Tortanus* or *Eurytemora herdmani* since these are exclusively American species. However, the preliminary results now given for *Centropages* and *Temora* would suggest that, provided due allowance is made for size differences, the oxygen requirements are similar for British and American specimens. Since the earlier results for *Calanus* were also of the same order it would appear necessary to re-examine the apparent difference in rate obtained for *Acartia*. Experiments comparing the Haldane-Dixon and Winkler methods on American *Acartia clausi* might be helpful.

In the majority of cases where experiments were conducted at two temperatures (*Tortanus*, *Centropages*, *Pseudocalanus*) the results suggested some increase in respiratory rate between 15°C and 20°C. This agrees with the results obtained on *Calanus* (Marshall *et al.* 1935, Clarke and Bonnet 1939, etc.) and on neritic species by Gauld and Raymont (1953) and Conover (1956). There was however one marked exception: *Eurytemora herdmani* showed no increase in respiratory rate between 15°C and 20°C. This result appeared to be equally true for males and females (Tables 6 and 7). The *Eurytemora* used in these experiments were all taken in hauls only north of Cape Cod in comparatively cold water. Specimens were not obtained from hauls from Woods Hole, whereas other copepods investigated were taken both in the colder and warmer water north and south of Cape Cod. Wilson (1932) quotes Fish as finding *Eurytemora herdmani* in Woods Hole Harbour, but most of the records (cf. Bigelow 1926, Wilson 1932) suggest that this neritic species is generally more to the north of Cape Cod. It is possible therefore that a temperature of 20°C was beyond the optimum for this species and that the copepod does not normally experience this temperature under natural conditions. Although the copepod was not killed by a short three-hour exposure to 20°C it is suggested that its respiration was maximal at lower temperatures.

The relation between oxygen requirements and size in copepods has been discussed by several workers. Conover (1956, 1959) considers that weight may be a better index of size than surface. Raymont and Gauld (1951) and Gauld and Raymont (1953) have, however, obtained fairly good agreement between respiratory rate and surface area using the formula

$$\log R = 2.19 \log L - 0.928,$$

where R is respiratory rate at 17°C and L is cephalothorax length.

From the mean respiratory rates of the seven species of American copepods investigated, a new regression equation may be derived relating respiratory rate to cephalothorax length: $\log R = 2.08 \log L - 0.827$, where R is respiratory rate at 15°C. A comparison of the experimentally determined rates and the rates calculated according to this formula (Table 8) suggest that although respiratory rate appears to be fairly closely related to surface area, there are considerable discrepancies between the observed and calculated rates for certain species. Thus the rates for *Pseudocalanus* and *Centropages hamatus* appear to be low, while those for *Tortanus*, *Metridia* and *Eurytemora* ♀ ♀ are high.

One difficulty is that such an equation takes no account of variations in the shape of cephalothorax in relation to surface area. It has been already shown by Gauld and Raymont (1953) that in some species a

TABLE 8. *The average respiratory rates of some calanoid copepods at 15°C as determined experimentally and as calculated according to the equation log R = 2.08 log L − 0.827*

	Respiratory rate (μLO_2/cop./hr)	
	Determined	Calculated
Metridia lucens	0.315	0.297
Tortanus discaudatus	0.275	0.233
Centropages typicus	0.157	0.155
Temora longicornis	0.147	0.138
Centropages hamatus	0.137	0.168
Eurytemora herdmani ♀	0.129	0.109
Pseudocalanus minutus	0.104	0.144
Eurytemora herdmani ♂	0.088	0.082

different shape of cephalothorax makes it necessary to apply a correction before applying their original equation to calculate respiratory rate. A similar correction should perhaps be applied to female *Eurytemora herdmani*. The experimental rate for female *Eurytemora* was distinctly high, and this may have been partly due to the respiration of the egg sacs attached to females for which no allowance was made. But female *Eurytemora herdmani* also have characteristic posterior projections at the end of the metasome and this presumably would alter the surface area/length relationship. Similarly for *Temora* no allowance has been made for the different shape of cephalothorax. The somewhat high respiratory rate for *Metridia* (Table 8) cannot be discussed very seriously as very few experiments were conducted on this copepod, and the animals were measured in only one.

It might be worthwhile to compare critically the experimental rates for *Centropages*, *Pseudocalanus*, and *Tortanus*, with rates calculated according to the original formula of Raymont and Gauld (1951), log $R = 2.19 \log L - 0.928$, since the cephalothorax shape in these species is elongate and cylindrical and therefore the formula might be applicable. It happens too that more experimental determinations are available for these three species, so that the results are more reliable.

The data for *Centropages hamatus* give a mean value of 0.137 μLO_2/cop./hr at 15°C and 0.172 at 20°C. At 17°C the rate would thus be *ca.* 0.151 μLO_2/cop./hr. The calculated rate at 17°C for *Centropages* of length 1.061 mm is 0.134 μLO_2/cop./hr, so that there is a fairly reasonable measure of agreement. For *Pseudocalanus* the estimated respiratory rate for copepods of mean length 0.984 mm at 17°C would be 0.114 μLO_2/cop./hr. This compares very well with the experimental values obtained of 0.104 at 15°C and 0.139 at 20°C, giving a rate at 17°C of ca. 0.118 μLO_2/cop./hr. The respiration rate of *Tortanus*, however, is much higher than would be expected from the calculated value. At15°C the mean rate was 0.275 μLO_2/cop./hr, and at 20°C 0.324, giving a rate at 17°C of ca. 0.295. The calculated rate at 17°C is only 0.189 μLO_2 /cop./hr.

In the case of *Temora* Gauld and Raymont (1953) suggested that in view of the shape of the cephalothorax the length must first be multiplied by 1.2 before using the usual formula. For American specimens of *Temora* the calculated rate at 17°C for specimens of length 0.965 mm becomes 0.162 μLO_2 /cop./hr, which compares favourably with an experimentally obtained value of 0.147 at 15°C.

In summary it may be claimed that bearing in mind variations in surface area due to changes in cephalothorax shape (*e.g.*, *Temora* and possibly female *Eurytemora*) the relation between surface area and respiratory rate appears to hold fairly well for the species investigated, with the exception of *Tortanus*. In this species the rate found experimentally is much higher than that calculated according to Raymont and Gauld's formula. It has already been suggested from observations on feeding that *Tortanus* is almost certainly carnivorous, and it would appear probable that the species has a considerably higher oxygen requirement in connection with this carnivorous habit. Some experiments on the oxygen requirements of other well-known carnivorous members of the zooplankton are now in progress.

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Light Adaptation by Marine Phytoplankton[1]

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ABSTRACT

Photosynthesis-light intensity curves were obtained for natural phytoplankton populations in the Sargasso Sea from surface waters and from depths to which 10% and 1% of the surface light penetrated. In winter, when the water was isothermal and mixed to depths below the euphotic zone, phytoplankton from all three depths behaved like "sun" forms, becoming fully light saturated at 5000 foot candles. In summer, when the water and plankton were stratified, the surface plankton were similar to the winter plankton, those from the 1% light level behaved like "shade" plants, becoming light saturated below 1000 foot candles, those from the 10% light level were intermediate in their response to light. The effect of light adaptation on the calculation of primary production from chlorophyll and light is discussed.

INTRODUCTION

The distinction between plants which are adapted to living at high and low light intensities is a familar one. These so called "sun" and "shade", or "heliophillic" and "umbrophillic", forms have certain distinguishing characteristics which are usually, though not always, consistent. Thus, the "sun" forms normally contain less chlorophyll, photosynthesis becomes light saturated at higher intensities, and their assimilation number (photosynthesis per unit of chlorophyll) is frequently lower at all intensities. These characteristics are found in different species which inhabit different types of environment (*i.e.* desert vs. forests), in individuals of the same species conditioned respectively to high and low light intensities, and even in "sun" and "shade"adapted leaves of the same plant. A partial review of this subject may be found in Rabinowitch (1951).

Most of the known examples of these phenomena are restricted to the higher plants and macroscopic algae. There have been fewer studies of light adaptation by unicellular algae and, though the distinction is often assumed to exist, evidence is almost lacking for natural phytoplankton populations. Steemann Nielsen (1934) described species of the dinoflagellate genus *Ceratium* which were found characteristically in deep ocean waters (*i.e.* 100 meters), while others were found only at the surface. He termed these "shade" and "sun" species respectively, and compared the morphology of the "shade" forms with umbrophillic forest tree leaves. His observations on the distribution of these species were later confirmed by Graham and Bronikovsky (1944). Rodhe *et al* (1958) concluded that the phytoplankton in Lake Erken adapts seasonably to changing light conditions, the summer species being more typical of "sun" forms, the winter population being shade adapted and light inhibited at the surface even at the low intensities encountered in mid-December in Sweden (*i.e.* 15 g cal/cm^2/day as compared with 700 g cal/cm^2/day for clear summer days). One of the present

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authors (Ryther, 1956) obtained photosynthesis-light intensity curves for a variety of marine phytoplankton cultures. In general the green algae, the diatoms, and the dinoflagellates respectively become both saturated and inhibited at progressively higher light intensities. In this sense these three groups could be considered as "sun", "intermediate" and "shade" forms, though the distinction is ecologically meaningless since they frequently coexist in the same environment.

Using natural surface phytoplankton populations Steeman Nielsen and Jensen (1957) made a series of photosynthesis-intensity curves during the *Galathea* expedition. Their curves for tropical ocean waters were extremely consistent and remarkably similar to the mean curve for all species examined in the culture experiments of Ryther described above. A similar series from the Tasman Sea in mid-summer, however, showed the phytoplankton to be more shade adapted, light saturation being reached at about 1,000 foot candles rather than the 2,000–2,500 foot candles for the tropical waters. Later studies by Steemann Nielsen and Hansen (1959) in the North Atlantic revealed that the surface plankton of this region were comparable to those of the Tasman Sea. However, samples from depths to which only 1% of the surface light penetrated (30–50m) showed quite different characteristics, becoming light saturated at intensities below 500 foot candles. These deeper organisms were described by Steemann Nielsen and Hansen as "shade plankton". In contrast to this, they found no differences in the light curves of phytoplankton from all depths sampled at the mouth of the Godthaab Fjord, where tidal currents caused a pronounced vertical mixing.

While the publication of Steemann Nielsen and Hansen was in press, the present authors were engaged in somewhat similar studies in the Sargasso Sea off Bermuda. The results which will be reported below will be largely a confirmation of the experiments described by the Danish scientists. However, they include more detailed ancillary data and are of particular interest because of the contrasting hydrographic conditions, the varying distributions of phytoplankton, and the resulting differences in the intensity and duration of light intensities to which the plants are exposed at different times of the year in these waters.

During the "winter" (November–April) the Bermuda offshore surface waters are isothermal and apparently well mixed to depths as great as 400 meters and always in excess of 150 meters. The chemical and biological properties of this mixed layer, including the phytoplankton, are very nearly homogeneous. For the rest of the year, the water is thermally stratified with a well developed, seasonal thermocline in the upper 25–50 meters. Under these conditions, the surface waters become nutrient impoverished and extremely poor in phytoplankton. However, a maximum of chlorophyll characteristically develops at a depth of 100–150 meters, just at the lower limit of the euphotic zone (1% of the surface radiation penetrates to about 100 meters in these waters). J. H. Steele and C. S. Yentsch (unpublished data) have recently investigated the causes of this chlorophyll peak, which appears to occur very commonly in other regions where the surface waters are thermally stratified. They proposed that this peculiar distribution results from a reduction in the rate of sinking of nutrient-deficient phytoplankton on encountering the richer water below the euphotic zone. The mathematical model which Steele developed to describe this phenomenon was substantiated by experimental evidence in which the settling rate of nutrient-deficient diatoms was greatly retarded by enriching the cultures.

Figure 1 shows vertical profiles of temperature and chlorophyll under typical unstratified ("winter") and stratified ("summer") conditions in the Sargasso Sea off Bermuda. While the rates of vertical circulation in winter are unknown, it seems reasonable to assume that the phytoplankton within the mixed layer would all be exposed to approximately the same average light conditions and would be circulated rapidly enough to prevent their being conditioned to the light intensity at any one depth. In

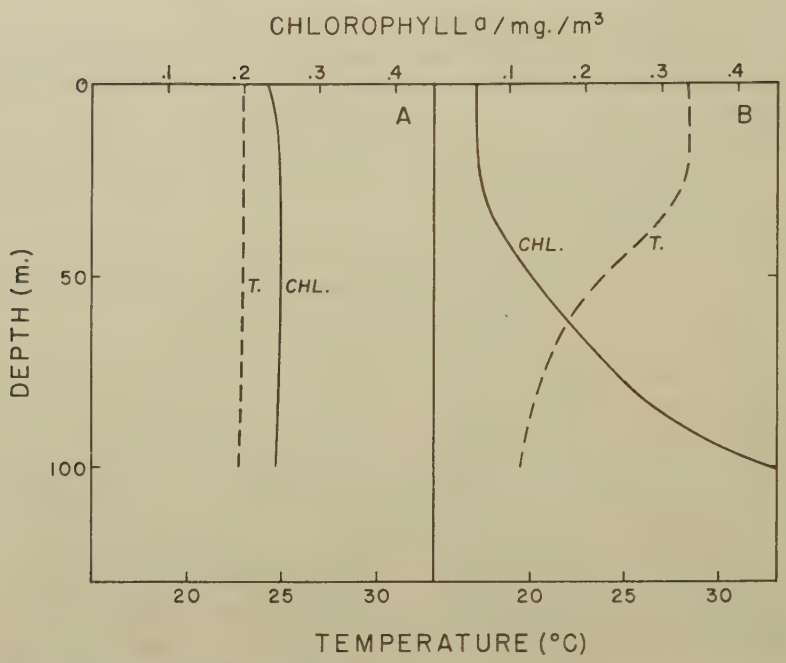

FIG. 1. Depth profiles of chlorophyll a (chl) and temperature (T) in November (A on left) and October (B on right) in the Sargasso Sea off Bermuda.

contrast to this, the vertical circulation in summer may be assumed to be negligible and the phytoplankton hence exposed for relatively long periods to the light conditions where they are found. These conditions provided an excellent opportunity to examine populations of the same species of phytoplankton held under extremely different natural illumination for evidence of a physiological light adaptation. Of particular interest was the comparison between the surface phytoplankton and that comprising the deep chlorophyll peak, and the comparison between summer "stratified" and winter "mixed" populations.

EXPERIMENTAL METHODS AND RESULTS

The experiments described below were carried out on November 14 and on October 4 and 15, 1958 when conditions were similar to those shown in Figures 1A and 1B respectively. Water was collected with a non-metallic sampler from the surface, 50 and 100 meters, where corresponding light intensities were equivalent to 100%, 10% and 1% of the incident surface radiation, as determined with a submarine photometer. Each sample was dispensed into a series of five 150 ml glass stoppered bottles to which were added approximately 15 μ curies of $C^{14}O_3^=$. The bottles were then placed in an incubator cooled with running surface water and covered with a series of neutral density filters which transmitted respectively 100%, 50%, 25%, 10% and 1% of the incident radiation. The experiments lasted for approximately four hours consisting of the two hours before and the two hours after solar noon. During this period, solar intensities are not only greatest but vary by only about 10% under clear skies. Solar radiation was recorded during the experimental periods with an Epply pyrheliometer, and the mean intensity received by the bottles was calculated for each experiment.

After exposure the contents of each bottle was filtered through an HA millipore filter. The filters were washed with 10 ml of 0.001 N HCl in a 3% NaCl solution, dried in a desiccator, and their radio-activity determined in a gas flow Geiger counter. The activity of each sample was taken as an index of relative photosynthesis.

The results of these experiments are shown

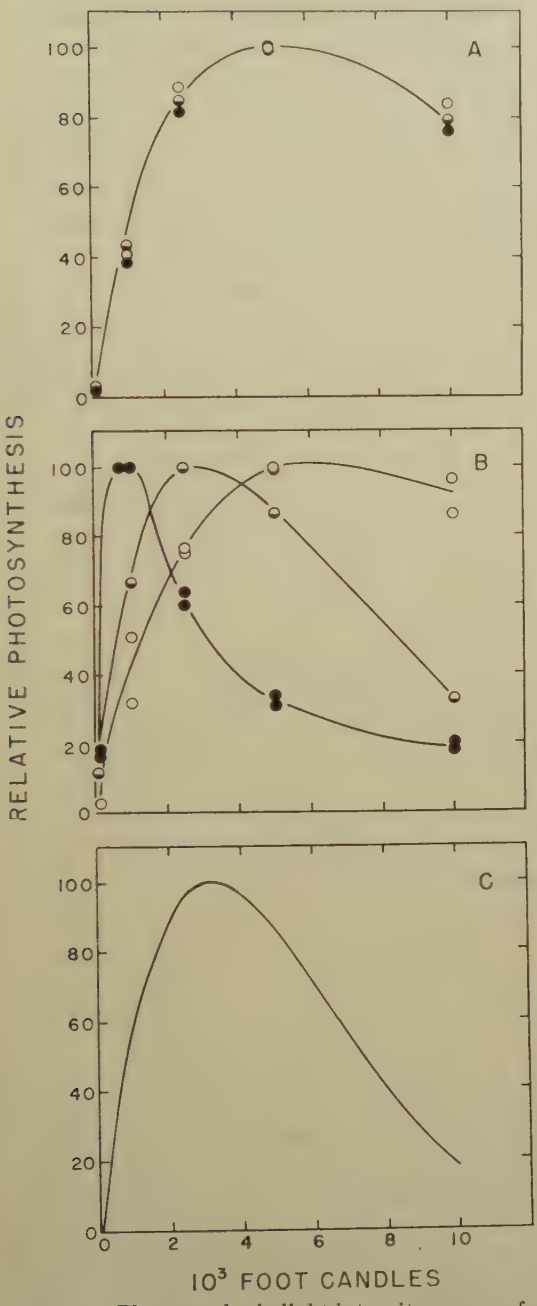

FIG. 2. Photosynthesis-light intensity curves of Sargasso Sea phytoplankton from depths to which 100% (open circles), 10% (half-filled circles) and 1% (filled circles) of the surface light penetrated in November (A top) and October (B center). C (bottom) is mean curve for phytoplankton cultures from Ryther (1956a).

in Figure 2; A being the series of curves from the three depths on November 15 when the water was mixed to below 100 meters, and B the similar curves on October 4 and 15 (two complete series on each day) when the water and plankton were stratified. Figure 2 C is the mean curve of all the experiments with cultures of marine phytoplankton as reported by Ryther (1956b).

Under the "winter" conditions, the phytoplankton at all depths within the euphotic zone showed the same relationship to light intensity. Surprisingly, the plants behaved as "sun" species, becoming fully light saturated at 5,000 foot candles, reaching half this value at 1,200 foot candles.

In October, three distinct curves were obtained with phytoplankton from the three depths. Those living in the surface waters, again acting as "sun" forms, behaved essentially the same as did the winter plankton from all depths. The phytoplankton collected from 50 meters (10% light) were intermediate in their response to light and their photosynthesis-intensity curve is almost identical to the average curve obtained with cultures (Figure 2 C). The plankton from 100 meters (1% light), on the other hand, behaved like "shade" plants, reaching light saturation below 1,000 foot candles.

DISCUSSION

The photosynthesis-light intensity curve obtained from algae cultures, reproduced in Figure 2 C, has been used in conjunction with chlorophyll concentration for calculating the natural rate of photosynthesis of marine phytoplankton (Ryther and Yentsch, 1957). This method assumes a constant assimilation number (photosynthesis per unit of chlorophyll at optimal light intensity) which is corrected for the natural light intensity from the ps-light curve, incident radiation, and submarine light penetration data.

This average curve obviously does not describe the behavior of the Sargasso Sea winter phytoplankton, which we have described as more typical of "sun" plants. However, a roughly bell shaped curve of this type, whether displaced to the right or left, is somewhat self-adjusting in that more

or less photosynthesis at lower intensities is to some extent compensated by the reverse at higher intensities.

The curve in Figure 2 C is still a good average description of the behavior of phytoplankton within the whole euphotic zone in summer. However, the use of an average curve in this case would be quite misleading for it would result in the under estimation of photosynthesis both in the surface waters where intensities are high, and in deep waters where intensities are low. In other words, it does not take into consideration the light adaptation of both surface and deep plankton.

The broken curve in Figure 3 shows a hypothetical depth profile of daily photosynthesis in midsummer (820 langleys/day incident radiation), assuming a phytoplankton population evenly distributed with depth. This curve was calculated from Figure 2 C and actual radiation data as recorded at Newport, R. I. on June 17, 1954, and is a reproduction of Figure 5 in Ryther (1956b). The solid line in Figure 3 is a recalculation of the same profile using, in place of Figure 2 C, the three curves in Figure 2 B. As discussed above, daily photosynthesis at both the upper and lower limits of the euphotic zone is higher due to

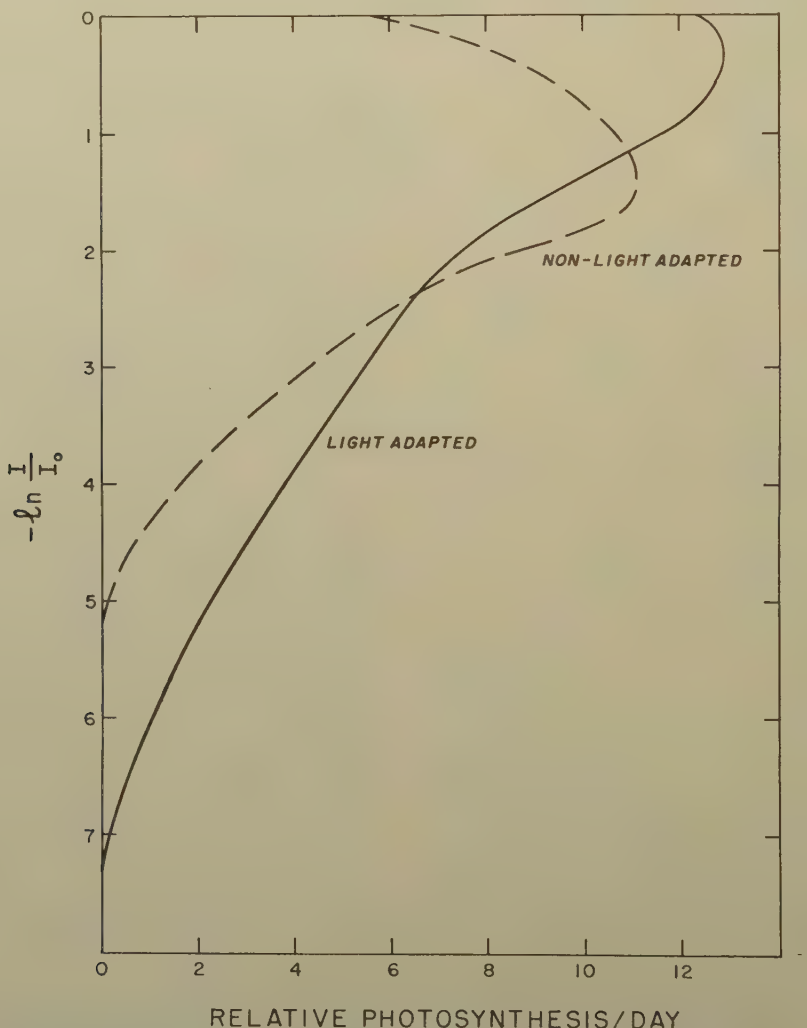

FIG. 3. Hypothetical depth profiles of daily photosynthesis by non light-adapted phytoplankton (calculated from Fig. 2 C) and light-adapted phytoplankton (calculated from Fig. 2 B).

light adaptation of the plants at these depths, while that at the intermediate depth remains nearly the same. The resulting daily rate of photosynthesis beneath a square meter of surface (*i.e.* the area of the curves in Figure 3) is some 30% greater for the light adapted algae. Under natural summer conditions, a greater discrepancy could be expected, since most of the phytoplankton occur near the lower limit of the euphotic zone (Figure 1B).

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Infra-red Observation and Cinematography of Microcrustacea

The purpose of this note is to present a simple illumination system for observation or photography of small semi-transparent animals such as microcrustacea. This system of illumination makes semi-transparent organisms appear as dark silhouettes on a light field. Use of the near infra-red spectrum permits observation and photography of experimental animals in extremely dim light or in total darkness. An observation and recording technique which is independent of ambient visible intensity is a distinct advantage in the study of dark adaptation or general behavior patterns of many pelagic plankters which behave very differently in different light intensities. Infra-red movies are used to establish the existence of various behavior patterns by the usual correlations of linear and angular velocities with intensities and gradients of the several physical and chemical parameters of the environment.

The illumination system is shown in Figure 1. It is directly comparable to Köhler illumination with the microscope. The lens *B* performs the same function as the microscope condenser, with the result that the light source is seen to be the same size as the condensing lens.

The light source *A* is a Westinghouse 500-watt photospot RSP-2 immersed in a mineral oil bath for absorption of the unwanted longer infra-red wavelengths largely responsible for heating. Visible radiation is excluded by use of a six-inch square black glass filter $\frac{5}{16}$ of an inch thick.[1] Black Carrara glass filters compare favorably in transmission with commercially available glass infra-red filters and appear considerably more resistant to fracture from heat or mechanical shock. The black glass filter is clamped to the oil bath against an "O" ring seal or any other suitable gasket for retaining the oil in the bath. An oil expansion reservoir must be provided since the oil becomes quite hot during the operation of the lamp. The oil reservoir should be three inches in diameter and about six inches high. The hole into the oil bath from the expansion reservoir should be about three inches in diameter as a safety precaution in the event of implosion of the lamp. For long periods of operation such as with an infra-red viewing device, a copper cooling coil connected to the coldwater tap should be included in the oil bath. Satisfactory intensities in the photographic infra-red spectral band (7500–12,500 Å) are obtained from this light source when the lamp is operated at 3250 degrees Kelvin.

The light source *A* in Figure 1 is located at one focal point of the condensing lens. The aquarium of experimental animals *C* is placed next to the condensing lens, and the camera or observers eye is placed at the other focal point *D*. The effect of such a system of illumination is to image the light source at the camera lens or observers eye where the imaging lens is seen brightly illuminated with the aquarium and zooplankton silhouetted against the brightly lighted field of the lens. A 14 by 18 inch plastic Fresnel lens having a focal length of two feet is used for the condensing lens.[2]

If the aquarium is placed on the same side of the condensing lens as the camera or observer the experimental animals appear natural size but if the aquarium is placed on the opposite side the images of the experimental animals will be magnified in accordance with the well known ratio

$$\frac{\text{size of image}}{\text{size of object}} = \frac{\text{distance from lens to image}}{\text{distance from lens to object}}$$

Since the aquarium is quite close to the lens the images will appear virtual and erect.

A condensing lens is more efficient than frosted glass for background illumination since it gathers light from a large solid angle and focuses it on the camera lens, while frosted glass gives only the limited forward scatter of light incident upon it. In our experiments the light intensity at the camera lens is 10,000 times as intense with a condensing lens as with frosted glass. The distribubution of intensity in the forward scatter from ground glass is responsible for the non-uniform exposures of vignetting obtained when frosted glass is used as a diffusing background. Opal glass is only a little better. Neither opal glass nor frosted glass is practical as a background for wide areas close up to the camera.

Exposure of Eastman Kodak High Speed Infra Red Movie film at 16 frames per second with a stop opening of f 2.5 gives an optical density of 0.9 with normal development in Eastman Kodak Microdol. Such organisms as the almost completely transparent cladoceran, *Leptodora kindtii*, or the relatively transparent mysid shrimp, *Mysis relicta*, which are usually seen best by their own scattered light or through crossed polaroids can be photographed as silhouettes.

It is important to know that the infra-red radiation employed in this method does not stimulate the experimental animals. Although it is impossible to state categorically that infra-red fails to stimulate it is possible to state operationally that infra-red produces no unique behavior patterns, nor does it alter any existing behavior pattern thus far tested. Presumably any alteration of an existing behavior pattern must be achieved by some alteration in linear or angular velocity. We have, therefore checked for such changes.

[1] Black Carrara glass used for building facings and manufactured by Pittsburgh Glass Co., Pittsburgh, Pennsylvania.

[2] Edmund Scientific Co., Barrington, N. J.

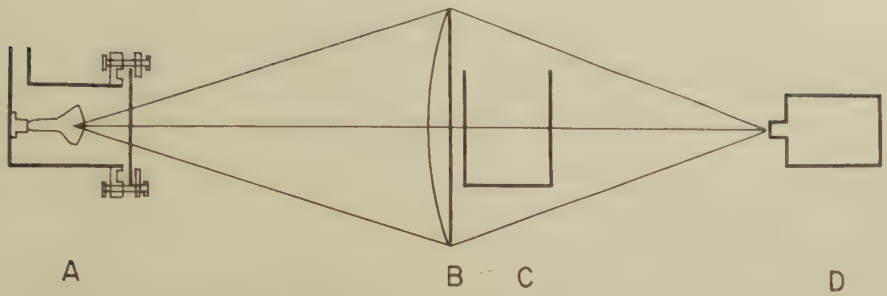

FIG. 1. Diagram of the illumination system: *A* is the light source; *B* is a 14 x 18 inch plastic Fresnel lens; *C* is the aquarium containing experimental animals; *D* is a movie camera.

To test for changes in linear velocity we invoked the null hypothesis that there is no significant difference in linear velocities in white light with and without infra red. Such a null hypothesis is amenable to the statistics of small samples.

The experiment was performed as follows. A population of *Daphnia magna* adapted to a given intensity of white light was continuously photographed with a movie camera for a period of thirty seconds. The animals were illuminated with white light for the first 15 seconds and with white light plus infra-red for the last 15 seconds. Analysis of the photographic record thus obtained shows an average linear velocity of 0.201 cm/sec. in white light and 0.196 cm/sec. in white plus infra-red. By the use of the Wilcoxon Sum for ranked differences of paired data, it was concluded that the mean differences of velocities are not significantly different from one another within the limits of the data.

Analysis of the same photographic record for angular velocities reveals an average angular velocity of 5 degrees/sec. in white light and 6 degrees/sec. in white plus infra-red. Again the use of the Wilcoxon Sum for the paired angular velocities indicates that they are not significantly different from each other within the limits of the data. The failure of *Daphnia magna* to respond to infra-red should not be extrapolated to other organisms without appropriate testing.

Finally, many behavior patterns are statistical in nature and are not readily observable over short periods of time. Such statistical behavior typically results in a net movement of a population in one direction to produce an aggregation at some given locus. The infra-red radiation employed in these studies whether with or without visible light failed to produce any aggregations of the population either toward or away from the source, or at the bottom of the container or at the surface of the water in a period of 2 hours.

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The Use of Carbon Dioxide to Construct pH Curves for the Measurement of Productivity[1]

INTRODUCTION

In recent years there has been increasing use of pH measurement for the determination of carbon metabolism in natural waters and in closed containers with living organisms (Verduin 1951, 1956a, 1956b; Jackson and McFadden 1954; Odum 1957a, 1957b; McQuate 1956; Park *et al.* 1958). A graph of pH against CO_2 is constructed for the particular water. The data for this graph are obtained either experimentally or by theoretical computation from alkalinity. Then the observed pH changes are converted into CO_2 changes by means of the graph. For some time, it has been apparent to us that one of the customary experimental procedures in this method leads to considerable error. The purpose of this note is to point out the error and suggest a better procedure applicable to both sea water and fresh water based on the use of CO_2 water.

In fresh water the theoretical equilibrium equations of Moore (1939) were used by Dye (1944) to compute nomograms so that with a known alkalinity, pH changes can be converted to CO_2 changes without actually determining the pH-CO_2 curve experimentally. In this work the alkalinity is determined by titration with a strong acid to approximately pH 4.5. Either a color indicator (such as methyl purple or methyl orange) or a pH electrode is used to locate the end point.

In sea water the constants in the equilibrium

[1] These studies were aided by the National Science Foundation through grant NSF G3978 on Ecological Microcosms.

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equations were determined by Buch and Wattenberg as summarized by Harvey (1957). With these constants for different salinities and temperatures, it is possible to compute a pH-CO_2 graph from alkalinity in sea water as well as in fresh water.

Because natural waters are not simple solutions containing CO_2 equilibria alone, it was considered advisable by Verduin (1956a) to refine the method, determining the pH-CO_2 curve by direct titration instead of by use of the theoretical equations and nomograms. This was an admirable advance since it was found that titration graphs were quite different and not readily predictable from alkalinity measurements alone. However, a conceptual error was involved which has affected many of the papers using this method, for example, Verduin (1956b, 1957), McQuate (1956), and Frey and Stahl (1958). As is well known, the titration curve of a strong acid and a weak base is quite different in shape from the titration curve of a weak acid and a weak base where there are common ions. Thus, when NaOH or HCl are used to obtain pH-CO_2 curves an erroneous assumption is introduced that an equivalent weight of strong acid or base is equal in effect on pH to an equivalent weight of CO_2.

METHODS

In order to provide a method for empirical determination of pH-CO_2 curves, and to show the error in using strong acids or bases, a titration was carried out with CO_2 water. Distilled water was allowed to come into equilibrium (both temperature and saturation) with a pure CO_2 atmosphere. The gas was bubbled through the water and, being heavier than air, was presumed to displace the air above the water in a two-liter Erlenmeyer flask. Thus, the water was assumed to be approximately in equilibrium with the CO_2 at one atmosphere pressure and at the measured temperature. For further refinement of the method, the CO_2 content of the water should be directly determined by an independent method. Saturation where bubbles are used is not likely to be exact.

From tables of CO_2 saturation in The Handbook of Chemistry (Lange 1952), the moles of total dissolved CO_2 per ml were computed. The CO_2 water was then introduced under the surface of a 100-ml sample of natural water by means of a volumetric pipette. pH was measured against added CO_2. Stable pH's were achieved approximately 5 seconds after the introduction. Bubbles of gas were rising through the flask of distilled water at all times. To avoid any unknown effects of suspended particulate matter, all samples of natural waters were first "Millipore" filtered. Initial high pH was obtained by use of N_2 gas to clear the sample water of free CO_2 before starting the titrations.

RESULTS AND DISCUSSION

Four graphs of pH against CO_2 were obtained with this method for a hard natural spring water and for a coastal sea water. Since these graphs were essentially identical, only one is given for each type of water. Figure 1 is a representative graph for the spring water and Figure 2 is one for the marine water. Also plotted in Figures 1 and 2 are the curves produced by titrations of the same waters with a strong acid (0.02 N H_2SO_4). The dashed curve in Figure 1 is the theoretical

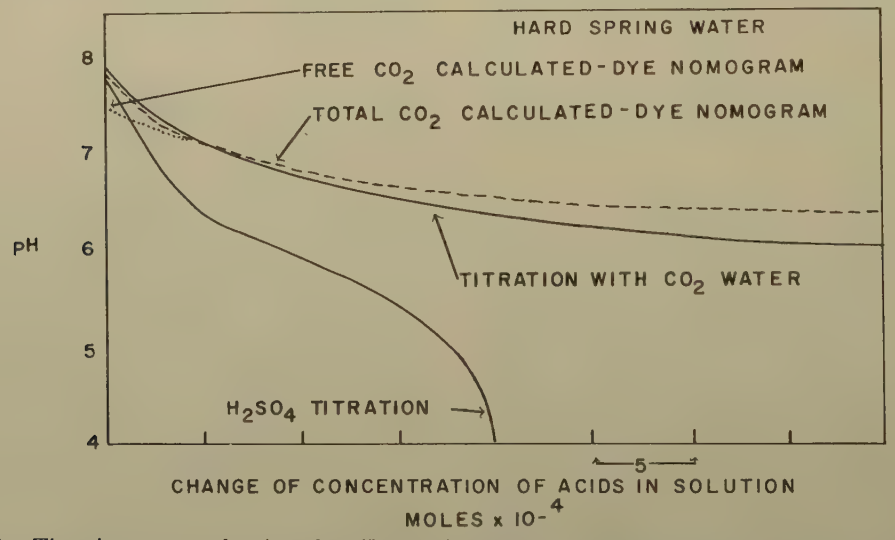

FIG. 1. Titration curves showing the pH as a function of acids added to hard spring water from San Marcos Spring, San Marcos, Texas. Temperature 28°C. Titration curves are given for sulfuric acid and water saturated with carbon-dioxide. The moles total carbon-dioxide calculated in solution are plotted as a function of pH as estimated with Dye nomograms. The dotted line is the free carbon-dioxide present at each pH.

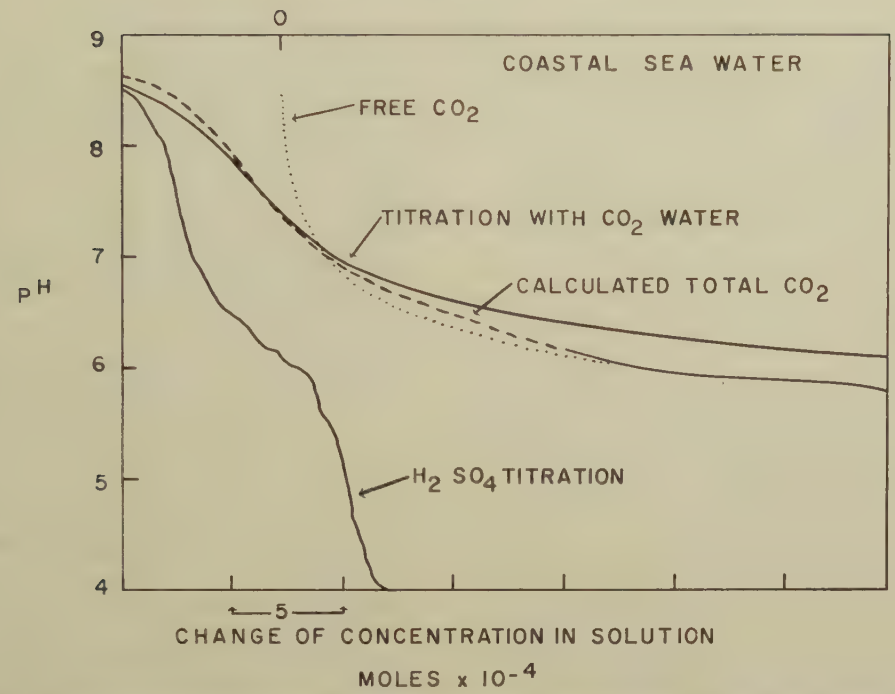

FIG. 2. Titration curves showing the pH as a function of acids added to sea water from a bay near Port Aransas, Texas. Temperature 28°C. Curves as in Figure 1.

curve determined with a Dye nomograph (Dye 1944). The dashed curve in Figure 2 is the theoretical curve computed from constants given by Harvey (1955).

The theoretical curve is similar to the curve determined with CO_2 water, but as expected on theoretical grounds, the titration curve of the strong acid is of entirely different shape. Metabolic rates computed by previous workers with strong acid curves may be in error in being too small.

At pH's below 7.5, increases in total CO_2 lead to increases in free CO_2 of the same amount. Thus the curves of pH and free CO_2 have the same general slope as curves of pH and total CO_2. As pH approaches 8, shifts in alkalinity equilibria occur so that curves of pH and free CO_2 have a different slope from curves of pH and total CO_2. The difference in total CO_2 and free CO_2 (dotted line) may be observed in Figure 2 for sea water. In studies of metabolism it is the total CO_2 that one is interested in measuring. Where data on diurnal free CO_2 changes have been used for computations of metabolism and respiratory quotient (Odum 1957a, 1957b), values are only approximate where the pH approaches 8.

Another example of a titration curve of CO_2 and pH is provided by McFarland and Norris (1958) in a paper that describes the pH changes taking place in enclosed vessels containing marine fish. In this case the fish provides a steady CO_2 supply which was computed from its metabolism. The pH-CO_2 curves thus provided are similar to those in Figures 1 and 2 obtained with artificial CO_2 water. Oppenheimer and Kornicker (1958) injected CO_2 gas into sediments and also obtained similar titration curves of marine sedimentary materials.

Thus it may be concluded that the pH-CO_2 curve method for measuring natural metabolism in free water is effective and empirically simple with the carbon-dioxide water procedure both in marine and fresh waters. Production and respiration values in a number of the previous papers involving titrations with strong acid or base are probably too small and should be recomputed.

Some have criticized the pH method for sea water on the grounds that the considerable alkalinity leads to an insensitive measurement (Ryther 1956). On the other hand Wells (1922) and Park *et al.* (1958) have found that coastal waters provide distinct diurnal curves for computation of carbon metabolism. These curves are even more easily obtained with the sensitive instruments presently available. Comparisons of metabolism in oxygen bottles and in free water (Odum and Hoskins 1958) indicate that bottle measurements are 2 to 100 times too small in shallow water. If bottle procedures such as the Winkler oxygen and radio-carbon light and dark bottle methods are not representative in shallow systems, then carbon metabolism is best measured with free water pH or oxygen methods. The diurnal measurement of metabolism with pH and

CO_2 has two great advantages over diurnal oxygen measurements: (1) No diffusion correction is ordinarily necessary with CO_2 curves; thus CO_2 curves reveal the course of night respiration (Park *et al.* 1958). (2) pH measurements are not as susceptible to pollution interference as are oxygen measurements by the Winkler process. However, both oxygen and pH curves are necessary for full interpretation of community metabolism.

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Memorial Resolution Respecting Dr. Bell M. Shimada and Townsend Cromwell, Esquire

Many members of the Society and other readers of Limnology and Oceanography will wish to endorse the memorial resolution of the Inter-American Tropical Tuna Commission which was made at their eleventh meeting in San Pedro, California on February 5, 1959.

Whereas, Dr. Bell M. Shimada and Townsend Cromwell, Esquire, were senior scientists on the staff on the Inter-American Tropical Tuna Commission since its early days

Whereas, their devotion to their researches and their outstanding abilities resulted in scientific contributions of great importance both to advancing basic knowledge in oceanography and marine biology and to the conservation of the living resources of the sea

Whereas, their scientific studies are of far reaching importance to the welfare of the fishing industries of the Americas

Whereas, these men lost their lives in the performance of their duties for the Commission. Now, therefore, be it

RESOLVED: That in the passing of Dr. Bell M. Shimada and Townsend Cromwell, the Inter-American Tropical Tuna Commission has lost two of the most important members of its scientific staff, marine science has lost two of its leaders, and the fishing industry of the American has lost two of its finest friends and supporters. Be it further

RESOLVED: That a copy of this resolution be incorporated in the Minutes of the Commission's Meeting, and copies thereof sent to their families and their associates.

American Institute of Fishery Research Biologists

The growth of population throughout the world is placing heavy demands upon our natural resources, including fisheries. Maintaining stocks of fish has become a critical necessity for many nations. The biological sciences must be directed to fisheries problems to answer this challenge and provide a sustained supply of fish for both the economic and recreational needs of the people.

To give substance and distinction to the vital field of fisheries biological research, a professional society known as the American Institute of Fishery Research Biologists was established and incorporated in the State of Washington on the 27th day of December 1956, by a group of nationally known fishery scientists of Canada and the United States.

The purposes of the Institute are:

1. To promote the conservation and proper utilization of fishery resources by advancing the theory and practice of scientific fishery biology.
2. To maintain high professional standards; to recognize achievement; and to adhere to a code to be known as "Principles of Professional Conduct for Fishery Biologists".

The Institute is organized like those representing other professions, such as the American Bar Association and the American College of Physicians. It provides for the election of Fellows, Members and Candidates.

The bylaws of the Institute provide for the regionalizing of Canada and the United States, each region having a vice president. Within each region there will be districts, each with its director. The regional vice presidents and district directors are members of a national Board of Control.

The national framework of the organization having been completed, the Institute is now designating local working districts. In response to a petition by Institute members residing in the northwest portion of the State of Washington, the Board of Control, consisting of W. F. Thompson, President, Seattle, Washington; Kenneth D. Carlander, Ames, Iowa; and John L. Hart, St. Andrews, New Brunswick, Canada have designated that area as a district. This is the initial district to be formed on the continent. Other areas in Canada and the United States are expected to follow suit.

At a dinner held in Seattle on June 1st the district was officially chartered.

Marine Biological Association of India

The Marine Biological Association of India was founded at Mandapam Camp, to promote interest in marine biology and other cognate sciences. The Association was formally inaugurated by the Honorable Mrs. Lourdhammal Simon, Minister for Fisheries and Local Administration, Madras State, on January 3rd, 1959. The following office bearers were elected: Dr. S. Jones (President), Prof. R. V. Seshaiya (Vice-President), Dr. R. Raghu Prasad and Dr. C. P. Gnanamuthu (Secretaries), Dr. R. P. Varma (Asst. Secretary), Shri. K. V. Rao (Treasurer), Dr. P. H. Ganapati (Editor), Dr. R. Subrahmanyan (Joint Editor), and Dr. S. V. Job (Managing Editor). The official organ of the Association, the "Journal of the Marine Biological Association of India", is expected to be issued half-yearly. Membership is open to all interested. All correspondence should be addressed to the Secretary, Marine Biological Association of India, Marine Fisheries P. O., Mandapam Camp, South India.

Research Grants

The Division of Biological and Medical Sciences of the National Science Foundation announces that the next closing date for receipt of basic research proposals in the Life Sciences is January 15, 1960. Proposals received prior to that date will be reviewed at the spring meetings of the Foundation's advisory panels and disposition will be made approximately four months following the closing date. Proposals received after the January 15, 1960 closing date will be reviewed following the summer closing date of May 15, 1960.

Inquiries should be addressed to the National Science Foundation, Washington 25, D. C.

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